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Vztah letokruhových řad k teplotním poměrům na západo-východním gradientu v pohořích střední Evropy

Tree-ring chronologies of Norway-spruce on west-east longitudinal gradient in the mountain ranges of central Europe

Disertační práce

Vedoucí disertační práce: Mgr. Václav Treml, Ph.D.

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Prohlášení:

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// Abstrakt

Globální změna klimatu může výrazně ovlivnit fungování jednotlivých ekosystémů, a to především těch, jejichž výskyt je teplotně podmíněn. Jedním z těchto ekosystémů je ekoton horní hranice lesa, významný vegetační fenomén vysokohorských oblastí, který vzniká postupným ústupem stromové vegetace s rostoucí nadmořskou výškou a klesající teplotou vzduchu.

Cílem předkládané disertační práce je vyhodnocení odezvy růstu smrku ztepilého (Picea abies [L.] Karst.) na měnící se klimatické podmínky v oblasti horní hranice lesa a přiléhajících lesů montánní zóny v oblasti střední Evropy.

Předkládané výsledky jsou založené na rozsáhlém datovém souboru obsahujícím téměř 1400 jedinců smrku ztepilého. Datový soubor dokládá těsnou závislost růstu stromů na teplotě aktuálního vegetačního období a také na teplotě měsíce října předcházejícího roku vzniku letokruhu. Hlavní rozdíly v odezvě růstu stromů ke klimatickým podmínkám jsou dány nadmořskou výškou, vliv expozice svahu vůči slunečnímu záření nebyl významný.

Růst stromů na horní hranici lesa v horských oblastech od Krkonoš po Nízké Tatry je ovlivněn zejména teplotami v měsících červnu a červenci. Tato závislost však nebyla v posledních 100 letech stabilní. Nízká koherence růstu v 50. letech 20. století byla způsobena teplým klimatem a změnou ve využívání krajiny. Naopak vysoká koherence růstu ve 30., 70. a 80. letech 20. století spolu s malým přírůstem souvisí s krátkými vegetačními obdobími a vysokým imisním zatížením.

Růstová odezva nebyla studována pouze na horní hranici lesa, ale i v horských lesích přiléhajících k horní hranici lesa. Bylo zjištěno, že teplotně limitované stromy na horní hranici lesa vykazují vysokou středně-frekvenční variabilitu růstu a silný vzestupný růstový trend od 80. let 20. století. Naopak lesní porosty z nižších montánních poloh vykazují relativně nízkou středně-frekvenční variabilitu a stabilní nebo mírně klesající letokruhový přírůst v posledním desetiletí. Zatímco porosty v oblasti horní hranice lesa profitují z nárůstu teplot, porosty v nižších oblastech citlivě reagují na sucho.

V rámci předkládané disertační práce byla také sestavena první letní teplotní rekonstrukce ze Sudet, která dosahuje až do roku 1700. Rekonstrukce dokládá obzvláště nízké červnové a červencové teploty na počátku 18. století, ve čtyřicátých letech 18. století a kolem roku 1820. Značně teplé klima se vyskytovalo v devadesátých letech 18. století a v posledních desetiletích.

Dendrochronologická analýza se ukázala jako účinný nástroj kvantitativního hodnocení odezvy horských lesních ekosystémů na změnu klimatu. Tato práce dokladuje, že růst smrku ztepilého v oblasti horní hranice lesa a v porostech přiléhající montánní zóny vykazuje značnou časovou a prostorovou variabilitu s velkým vlivem nadmořské výšky a polohou daného regionu na západo-východním gradientu ve střední Evropě.

Klíčová slova

dendrochronologie, ekoton horní hranice lesa, klimatická rekonstrukce, letokruhy, odezva růstu stromů, radiální růst, smrk ztepilý, střední Evropa, změna klimatu

Abstract

The Earth´s climate system has recently experienced substantial warming which likely impacts temperature-limited communities close to their distribution margins. The alpine treeline ecotone represents upper distributional limit of montane/subalpine forests. This biogeographic boundary relies mainly on decreasing temperature with increasing elevation. Surprisingly the response of treeline ecotone to ongoing warming has varied a lot and the reasons of this variability are poorly understood.

The aim of this dissertation thesis is the assessment of growth trends and tree ring response of Norway spruce (*Picea abies*[L.] Karst.) to climatic oscillations at treelines and montane forests of East-Central Europe. This dissertation deals with both inter-regional and intra-regional (aspect, elevation) variability of tree growth.

The presented results are based on an extensive data set of growth curves for almost 1400 trees. All study sites revealed close relationship between tree ring widths and growing season temperatures as well as the temperatures of October preceding to ring formation season. The main site-dependent differences in growth trends and temperature responses were attributed to elevation, the effect of aspect was relatively less significant.

At treelines between the Krkonoše Mts. and the Nízké Tatry Mts. we found that tree growth is driven mainly by temperatures of June and July, however the effect of these months was not stable during the last approx. 100 years. The period of low intra-regional growth coherency and higher growth than expected in the 1950s reflected warmer, less-limiting conditions and land use change. Highly coherent growth in the 1930s, 1970s and 1980s with prevailing narrow tree rings was related to the strong environmental growth-limiting signals of short growing seasons and high acid pollution loads.

Considering not only timberline but also montane forests, we found that temperature-limited trees in the upper montane zone adjacent to timberline exhibited high medium-frequency growth variability and a strong increasing growth trend since the 1980s. On the other hand, trees in the lower-montane zone displayed relatively low medium-frequency variability and a stable or slightly decreasing growth trend in the last decade. While timberline trees benefit from warming, trees from lower montane zone begin to be sensitive to drought.

Within this thesis the first summer temperature reconstruction from the Czech Sudetes Mountains that extends to 1700 AD was compiled. An ensemble reconstruction suggests particularly cold June-July temperatures at the beginning of the 18th century, in the 1740s and around 1820. Markedly warm conditions occurred in the 1790s and during the most recent decades.

Dendrochronology proved to be efficient tool for the quantitative evaluation of the response of mountain forests to climate change. This dissertation showed that growth of Norway spruce at treelines and montane forests has exhibited a substantial temporal and spatial variability with great influence of elevation and the position of a given region on a west-east gradient in East Central Europe.

Key words

climate change, climate reconstruction, dendrochronology, East-Central Europe, growth response, Norway spruce, radial growth, treeline ecotone, tree rings

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Introduction

Mountain forests offer a wide range of ecosystem services, e.g. carbon sequestration and storage, moderation of extreme climatic events, regulating the local climate and air quality, erosion prevention, genetic diversity, cultural services (e.g. M.A. 2005; TEEB 2008). Forests and especially mountain forests are, however, in many respects under the influence of the climate change when last decades have been warmer than any preceding decade since 1850 (IPCC 2014). The climate change is reflected in temperature increase, changes in precipitation distribution as well as in shifts in habitats´ geographical distribution (IPCC 2014). Alongside, global warming can cause forest ecosystems to either decrease in productivity from increased drought or increase in productivity from rising temperatures (Babst et al. 2013; Schuster, Oberhuber 2013). Therefore, tree growth responses to ongoing climate change are of a special importance as they sensitively track the pace and direction of climate change.

Temperature limited vegetation communities close to their distribution margins are especially vulnerable to climate change (Holtmeier 2009). Tree stands in treeline ecotone represent excellent examples of such communities. Alpine treeline ecotone belongs among the most prominent temperature-driven ecological boundaries (Körner 2007). Alpine treeline ecotone relies mainly on decreasing temperature with increasing altitude, associated with decline in the tree life form (Körner 1998), for which both the sink (or growth) limitation and source (photosynthesis, nutrients) limitation hypotheses have been offered as explanations (Körner 1998). Contemporary responses of treeline trees to climate change may differ due to regional variations in climate and the influence of local (non-altitudinal) factors including topography, competition, frequency of disturbances, anthropogenic impacts (Körner 1998; Holtmeier, Broll 2007; Harsch et al. 2009) and also topography-induced variability in near-ground temperatures (Körner 2007).

Tree rings provide possibility to study recent and past growth dynamics of trees in response to various environmental effects, particularly climatic conditions (Fritts 1976). Studying growth-climate responses of treeline trees through tree rings is therefore useful to discern recent dynamics of alpine treelines (Babst et al. 2013). Growth-climate patterns in the alpine treeline ecotone have been investigated in high-elevation forest zones of Central Europe, especially in the European Alps (e.g. Rolland, Petitcolas, Michalet 1998; Frank, Esper 2005; Büntgen et al. 2006, 2008) and the Carpathians (Bednarz et al. 1999; Savva et al. 2006; Büntgen et al. 2007; Sidor et al. 2015; Kaczka, Czajka, Łajczak 2015), however the Hercynian areas were before 2010, more or less, neglected.

Furthermore, the assessment of long-term effect of climate fluctuation on ecosystems beyond the instrumental measurement is needed and tree rings from treeline trees are a good proxy for summer temperature (Stenseth et al. 2002; Büntgen et al. 2011). Although the number of pre-instrumental temperature reconstruction is growing, temperature reconstructions from tree ring chronologies are established particularly from the Alps (e.g. Büntgen et al. 2006), Pyrenees (Dorado Liñán et al. 2012), Carpathians (Popa, Kern 2009; Büntgen et al. 2013; Popa, Bouriaud 2014) and Fennoscandia (Gunnarson, Linderholm, Moberg 2011; Esper et al. 2012). The number of temperature-sensitive tree-ring chronologies outside above mentioned highest alpine mountain ranges and high latitudes is very limited (Büntgen et al. 2010). The Sudetes Mts. are a region with scarce tree-ring data, spanning only the last two centuries (Sander et al. 1995; Brázdil et al. 1997; Treml, Ponocná, Büntgen 2012), and reliable instrumental temperature records from this region are missing for a large part of the 19th century (Migała 2005).

Since the Central European mountains are situated along west-east maritime-continental gradient (Mikolášková 2009) and second-order climatic factors play an important role in shaping treeline position (Treml, Migoń 2015), the tree ring response to climate change can vary along this gradient. However, the potential differences in responses of treeline and montane tree stands to climate change in Central Europe are unknown.

My dissertation thesis is focused on growth-climate response patterns of Norway spruce (Picea abies [L.] Karst.) along longitudinal and elevation gradients in Central Europe (the Sudetes Mts., the Babia Góra Mts., the Nízké Tatry Mts.). Norway spruce is the economically most important forest species native to mountain habitats of Central Europe (Spiecker et al. 1996), spanning a natural range from the montane zone up to treeline (Chytrý 2013).

The specific goals of this thesis were:

- to compare the response of tree ring widths to climatic variables along elevation gradients, in different slope aspects and along west-east zonal gradient,
- to detect altitudinal range where the tree growth is temperature limited,
- to create summer temperature reconstruction from the Czech Sudetes Mts.,
- to discern possible divergence of tree growth at treeline from temperature trends.

Recent state of art

The alpine treeline is the most conspicuous vegetation limit in high-mountain areas (Holtmeier 2009). Treeline represents a transition zone between the uppermost closed stands of montane forest and treeless alpine vegetation (Körner, Paulsen 2004). Possible causes for this transition have been widely discussed mainly in terms of ecophysiological mechanisms of treeline formation (Körner 1998; Wiley, Helliker 2012). All studies agreed that the altitudinal position of alpine treeline is determined mainly by temperature during the growing season (Fritts 1976; Tranquillini 1979; Körner 1999; Hoch, Körner 2009). Besides contemporary temperatures, additional factors affect the alpine treeline ecotone, such as influences of the past climate, other climatic variables than temperature (wind, drought), site history, terrain morphology, various types of slope processes (avalanches, rock fall), snow accumulation, biotic factors (e.g. herbivore browsing, grazing pressure), occurrence of fires and relations with other species (e.g. competition, facilitation), human activities (Holtmeier 2009; Körner 2007; Treml, Migoń 2015).

The treeline ecotone is mainly temperature limited and thereby could be a sensitive bioindicator of past and recent climate oscillations (Holtmeier 2009). The treeline ecotone is especially vulnerable to any alteration of the heat balance, in terms of both long-term temperature trends and their superimposed extremes (Lenoir et al. 2008). Global warming is expected to cause variation of treelines in position, structure, composition and productivity (e.g. Stenseth et al. 2002; Grace, Berninger, Nagy 2002; Camarero, Gutiérrez 2004; Holtmeier, Broll 2005).

However, the response of treeline ecotone position to climate warming is not universal and differs with different form of treeline ecotone (Harsch et al. 2009). Diffuse treelines respond to overall warming because they are strongly growth limited by low temperature. In contrast, abrupt, krummholz or island treelines were more likely to advance with winter warming in association with other constrains such as wind-induced damage, snow or winter desiccation (Harsch et al. 2009). Crucial factor of this advance is seedling mortality and dieback, because seedlings tend to be less tolerant to harsh conditions than mature trees due to their small root system, low stature and low biomass (Harsch, Bader 2011).

Tree growth responses to ongoing climate change are of special importance because forest ecosystems are one of the most productive components of the Earth’s biosphere (Pan et al. 2011). Cell walls of woody tissues represent a considerable sink of atmospheric carbon, with changes in wood formation playing an important role in the carbon cycle (Luyssaert et al. 2008). Global warming can cause forest ecosystems to either decrease in productivity from increased drought or increase in productivity from rising temperatures (Babst et al. 2013; Schuster, Oberhuber 2013). Negative and positive effects on forest productivity may even vary at local or regional scales, with particularly distinct differences occurring along altitudinal gradients (Mäkinen et al. 2002; King et al. 2013). Reconstructing the dynamics of forest productivity at decadal to centennial time-scales requires precise estimates of past growth trends (Melvin, Briffa 2008; Biondi, Qeadan 2008; Büntgen et al. 2012; Babst et al. 2014).

The growth of the Norway spruce in Europe is influenced by various climatic variables depending on geographic regions and site altitude. Generally, the limiting effect of low precipitation on Norway spruce growth decreased and the effect of air temperature increased with increasing latitude and/or altitude (Schweingruber 1996; Mäkinen et al. 2002; also e.g. Wilson, Hopfmüller 2001; Savva et al. 2006). In the intermediate elevation sites of temperate Europe, there is not any significant correlation with climatic variables meaning that spruce growth proceeds in optimal conditions (e.g. Mäkinen et al. 2002; Sidor et al. 2015).

Precipitation is the main factor limiting the tree growth at lower altitudes of Central Europe (e.g. Schweingruber 1996). Tree radial growth can be here influenced both by precipitation in the previous year and by precipitation in current year (e.g. Wilson, Hopfmüller 2001; Rybníček et al. 2009; Sidor et al. 2015). Precipitation in spring of the previous year and precipitation in winter, spring and summer of current year are of the highest importance (Fritts 1976; Kozlowski, Pallardy 1997). The influence of preceding year on the current growing seasons' growth results from the persistence of various effects into subsequent years through changes in nutrients and biological preconditioning of growth. The carry-over effect, such as photosynthetic gain, and storage of assimilates and water from the previous growing season, impacts current-year radial growth (Kozlowski, Pallardy 1997). Büntgen et al. (2007) reported a significant effect of February-April precipitation on tree growth in the Tatra Mts., and attributed this positive effect to the water supply at the beginning of the growing season. Others ascribe the positive influence of February precipitation to the protective effect of the snow pack, which prevents soil from freezing and decreases the risk of winter desiccation and/or fine-roots dieback (Tierney et al. 2001).

As opposed to low elevations, temperatures have been the one of the main factors governing radial growth in high elevation (e.g. Mäkinen et al. 2002). At high altitudinal level, tree growth is strongly limited by summer temperatures (e.g. Dittmar, Eißing, Rothe 2012; Mäkinen et al. 2002; Büntgen et al. 2007; Sidor et al. 2015). June-July is the period of most intense cell enlargement and thus the most important period for tree ring width (Cuny et al. 2015). Many studies (e.g. Mäkinen et al. 2002; Büntgen et al. 2007; Sidor et al. 2015 etc.) reported that tree ring width is positively influenced by the temperature in October preceding the ring formation season. The effect of preceding October on tree ring width is usually interpreted as the use of carbon reserves created in the end of the preceding growing season (Oberhuber 2004).

Several studies have investigated elevation-depend growth-climate responses e.g. in southwestern and eastern Germany (Mäkinen et al. 2002; Dittmar, Eißing, Rothe 2012), in the northern Alps (Leal et al. 2007; Hartl-Meier et al. 2014b, 2014a), in central Alps (Paulsen, Weber, Körner 2000; Vittoz et al. 2008), the Bavarian Forest (Wilson, Hopfmüller 2001; Čejková, Kolář 2009), the northern part of the Babia Góra Mountains (Bednarz et al. 1999; Kaczka, Czajka, Łajczak 2015), the Tatra Mountains (Savva et al. 2006; Büntgen et al. 2007), and the Carpathians (Kaczka, Büntgen 2007; Sidor et al. 2015). These studies generally report temperature-controlled radial growth at higher elevations, mixed effects of precipitation and temperature at middle elevations (around 700–1000 m a.s.l.), and drought-limited tree ring widths at lower elevations.

The impacts of environmental factors on the tree growth change gradually not only across altitudinal and latitudinal gradients, but also in response to changing continentality, usually along longitudinal gradient (Körner, Paulsen 2004). It is well known that the highest treeline positions are situated in continental regions, whereas treelines in maritime areas are located in relatively low elevations (Körner 1999).

As was introduced by Linderholm et al. (2003) higher growth variance and stronger response to climate was revealed in the oceanic area west of the Scandinavian Mts., compared to the more continental areas further east. Linderholm et al. (2003) also pointed gradual change in radial tree growth and response to climate along the maritime-continental gradient. Similarly, Babst et al. (2013) found coherent patterns in climate response depending upon ambient environmental conditions represented by latitudinal/elevational location. As was documented by Kašpar and Treml (2016) the highest-elevated treelines increased by approximately 94 m per 100 km between 10°E and 20°E in the Central Europe north of the Alps. This increase in treeline elevations with longitude is associated with rising isotherms of growing season temperatures towards east, a reflection of the increasing continentality and the mass of elevation effect of mountain ranges (Kašpar, Treml 2016).

Dendrochronological studies on Norway spruce in the region of interest

First available tree ring width chronologies of Norway spruce in the Krkonoše Mts, were established in the upper Labe Valley and were particularly used for dendroecological studies (Dobrý et al. 1992; (Sander et al. 1995; Sander, Eckstein 2001; Kroupová 2002). Within these studies the effect of air pollution on the tree growth was particularly investigated. Sander et al. (1995) realised that tree ring width (maximum latewood density as well) declined under severe pollution impact since 1965. Similar results were reported by Kroupová (2002). According to her study, the period of 1979–1989 was critical for spruce stands as indicated by extremely low increments reflected air pollution level in the Krkonoše Mts. Despite the heavy damage, spruce stands showed high regeneration capacity (Kroupová 2002).

Similarly, Godek et al. (2009) studied tree ring growth dynamics in the period of spruce-forest dieback and air pollution deposition in the Krkonoše Mts. They identified reduced vitality of spruce forest between 1965 and 1985 followed by systematic increase in increments. Improvement of forest conditions after 1985 was affected according to this study by gradual decrease of air pollution concentration and prolongation of the vegetative seasons connected with unusually warm two last decades of the 20th century.

Another dendroecological study was prepared in the Krkonoše Mts. (Kolář et al. 2015) with focus on tree growth depression in period between 1970s and 1980s and subsequent growth release. The main reason of the tree growth decline was acid deposition, from both sulfur and nitrogen compounds. During monitored period the health of the spruce stands in the Krkonoše Mts. declined and many missing rings were observed (Kolář et al. 2015). At the end of 1980s TRW recovery started which was most likely triggered by the combined effect of efficient pollution control and a warmer but not drier climate.

Also dendrogeomorphological research was conducted in the Krkonoše Mts. Dendrogeomorphological methods and procedures were used for dating and analysing snow avalanches (Tumajer, Treml 2015) According to this study, based on identification of abrupt growth changes, changes in stem eccentricity etc., totally 20 very probable and 29 probable avalanche events were dated during the period 1904–2012 which helped to expand the list of directly observed avalanches in the Krkonoše Mts.

First dendroclimatological study in the Krkonoše Mts. was carried out by Brázdil et al. (1997) who examined tree ring width and maximum wood density for the period 1804–1989. Temperature explained about 36% variability in tree rings. The greatest similarity between reconstructed and measured series was observed in the periods 1840–1870 and 1930–1950.

Treml et al. (2015a) investigated the differences in phenology of wood formation across the treeline ecotone and thermal characteristics in the Krkonoše Mts. They suggest that there were two periods with significant differences in wood phenology between timberline and treeline – at the beginning and at the end of the growing season, and that cambial activity significantly increased when soil temperature increased from near zero to a threshold temperature of 4–5 °C.

Kašpar and Treml (2016) evaluated how factors as maritime–continental gradients, the mass elevation effect, and varying distance between the treeline and summits influence treeline temperatures and treeline elevation. They showed that treeline temperatures in the Central Europe are similar to those in the Alps and that treeline elevation increases along the 50th parallel from 1100 m at 10°E to 1800 m at 20°E.

Kašpar, Hošek and Treml (2017) have recently tested the effect of wind speed on various growth metrics and the effect of wind speed on the possible treeline depression in the Krkonoše Mts. In treeline ecotone of the Krkonoše Mts. wind caused evident biomass loss, however radial growth was not significantly affected, and the effect of wind on height increment was limited only to parts of the stem from 2 m above ground (Kašpar, Hošek, Treml 2017).

In the treeline ecotone in the Jeseníky Mts. the effect of dwarf pine on Norway spruce was examined (Šenfeldr et al. 2014). It has been found that increasing density of dwarf pine stands strongly reduced vegetative propagation of spruce. In contrast, dense pine stands increased spruce height growth, presumably by providing shelter against wind and/or browsing.

The overall trend of treeline ecotone shifts in the Krkonoše Mts. and the Jeseníky Mts. (Sudetes Mts.) was studied by Treml and Chuman (2015) and Treml et al. (2016). They determined a pronounced treeline ecotone advance since 1930s. Enhanced tree establishment depended mainly upon agricultural land abandonment. Increasing summer temperatures had a negative influence on seedling establishment in the last few decades.

Site-dependent growth trends along an altitudinal gradient in the Krkonoše and the Jeseníky Mts. were presented by Treml, Ponocná and Büntgen (2012) and both in the Sudetes Mts. and the Babia Góra Mts. by Ponocná et al (2016). Treml et al. (2015b) also introduced first summer temperature reconstruction from the Sudetes Mts. that extends to 1700 AD (see section Main results).

Further regional dendrochronological studies of Norway spruce were also conducted in other mountain ranges of Czechia, e.g. from the Jizerské Mts. (Rydval, Wilson 2012), the Orlické Mts. (Rybníček et al. 2009), the Krušné Mts. (Kroupová 2002), the Hrubý Jeseník Mts. (Kroupová 2001) and the Moravskoslezské Beskydy Mts. (Šrámek et al. 2008; Rybníček et al. 2010; Čermák et al. 2010). All these chronologies were gained from spruce stands located in lower areas from 550 to 1000 m a.s.l. TRW chronologies from the Moravskoslezské Beskydy Mts. (Šrámek et al. 2008; Rybníček et al. 2010; Čermák et al. 2010) were characterized by a constant decrease in radial increment with noticeable growth depression in the second half of the 1970s and at the beginning of the 1980s. TRW was significantly affected by precipitation (monthly precipitation in July and September of the previous year and during the growing season, i.e. April-September) rather than temperatures (positive correlation was found with temperatures In October of the previous year and in March of the current year). In the Krušné hory Mts. (Kroupová 2002) an abrupt growth decrease of the Norway spruce was observed in the second half of the 1970s lasting until 1983. Contrary to the Moravskoslezské Beskydy Mts. and the Krkonoše Mts. tree ring growth was dominantly influenced by winter temperatures (January and February temperatures), May temperatures and also precipitation in July of the previous year. Radial growth in the Orlické Mts. (Rybníček et al. 2009) was depressed between the beginning of the 1970s and the end of 1980s. Variations in TRW were influenced by temperatures in July of the current year and precipitation sums in July of the previous year and also by precipitation in February and March of the current year. The only significant response of tree growth to temperature was identified from May to July in the Jizerské Mts. (Rydval, Wilson 2012), the influence of precipitation on growth was minimal. Moreover, tree growth displayed a significant reduction around 1980 which coincided with the period of greatest atmospheric sulfur concentration. This study also demonstrated that the effect of sulfur pollution on tree growth declined with distance from a point source of pollution.

In Western Carpathians, first dendrochronological studies were conducted at the Babia Góra and the Vysoké Tatry Mts., where Bednarz (1984, cit. in Bednarz et al. 1999) compared dendroclimatological reconstructions of summer temperatures from the Alps with these from the Tatra Mts. Bednarz et al. (1999) further carried out a dendrochronological analysis of Norway spruce in the Babia Góra Mts. Savva et al. (2006) explored growth/climate responses in stands along an altitudinal gradient ranging from 839 to 1468 m a.s.l. in the Tatra Mts. Similarly, Büntgen et al. (2007) analysed growth responses to climate of tree-ring width and maximum latewood density chronologies from the Tatra region in Poland and Slovakia. Büntgen et al. (2013) established temperature-sensitive tree-ring reconstruction from the same greater Tatra region (including Slovenský kras area). Moreover, Kaczka et al. (2016) developed temperature and precipitation reconstructions in the Tatra Mts.

Bednarz et al (1999) obtained 350 years long tree ring width chronology (spanned the years 1636–1989) from 46 specimens of Norway spruce in the subalpine area between 1150 and 1450 m a.s.l. in the Babia Góra Mts. Chronology positively correlated with June-July temperature and negatively with June-July precipitation. Furthermore, Bednarz et al. (1999) recorded the period with growth declines and growth increases, affected by climate except the decline in the period 1950–1980 which was caused by in the influence of air pollution.

Savva et al. (2006) identified positive relationships between current-year radial growth and mean monthly temperature in March, April, June and July in the Tatra Mts. With increasing elevation, the strength of this correlation declined for March-April and increased for June-July temperatures. Trees at the low-elevation sites responded positively to a warm early spring. Similar result was obtained by Büntgen et al. (2007) who recorded that site elevation and frequency of growth variation were significant variables explaining growth response to climate. It has been found that the ring-width chronologies correlated to June-July temperatures, whereas the latewood density chronologies were correlated with the April-September temperatures. Response to precipitation increased with decreasing elevation.

Material and methods

Geographical setting

The focal area for the study was in four mountain ranges with the main goal to cover west-east maritime-continental gradient within the East-Central Europe.

The study region is situated at 50° N latitude and between 15°E and 20°E longitude (Figure 1) and comprises the Krkonoše Mts., the Jeseníky Mts. (treated as one region comprising the Hrubý Jeseník Mts. and the Králický Sněžník Mts.), the Babia Góra Mts. and the Nízké Tatry Mts.

The Krkonoše Mts. (Sněžka 1602 m a.s.l.) and the Jeseníky Mts. (Praděd 1491 m a.s.l.) belongs to crystalline areas of the Bohemian massif and the Sudetes mountains, the Babia Góra Mts. (1725 m a.s.l.) belong to flysh areas of Western Outer Carpathians and the Nízké Tatry Mts. (Ďumbier 2043 m a.s.l.) represent crystalline and calcareous massif of the Central Western Carpathians.

Climate is cold and humid with annual precipitation totals ranging from 1200 mm in the Jeseníky Mts. to 1500 and 1800 mm at summits of the Babia Góra Mts. and the Krkonoše Mts., respectively (Kwiatkowski 1982; Obrebska-Starkel 2004; Migała 2005). Soils of the montane forests are mostly podzols, dystric cambisols, and rankers (Tomášek 1995; Granec, Šurina 1999).

Mountain forests between 900 m a.s.l. and the treeline ecotone are primarily composed of Norway spruce (Picea abies [L.] Karst.), with the upper limit of closed forest (i.e. the lower boundary of the treeline ecotone) located around 1240–1400 m a.s.l. Prostrate dwarf-pine (Pinus mugo) is also widespread in treeline ecotone except the Jeseníky Mts. (where it was planted, however).

The lower limit of alpine treeline ecotone (i.e., so called timberline) is increasing toward east from 1240 m in the Krkonoše Mts., 1320 m in the Jesníky Mts. up to ca. 1370 m in the Babia Góra Mts and 1410 m in the Nízké Tatry Mts. with maximum timberline positions about 100 m higher than above-mentioned mean values (Treml, Migoń 2015; Czajka et al. 2015; Czajka, Łajczak, Kaczka 2015a), Table 1). In the second half of 20th century and recently, treeline ecotones have been gradually advancing upwards in consequence of cessation of land-use and warming (Weisberg, Shandra, Becker 2013; Czajka, Łajczak, Kaczka 2015b; Treml et al. 2016). During the 1970s and 1980s, forests of the study area were affected by acid pollution resulting in growth depression, which was most pronounced in the western part of the study area (Kroupová 2002; Sander et al. 1995; Kolář et al. 2015).

Figure 1: Location of the study areas

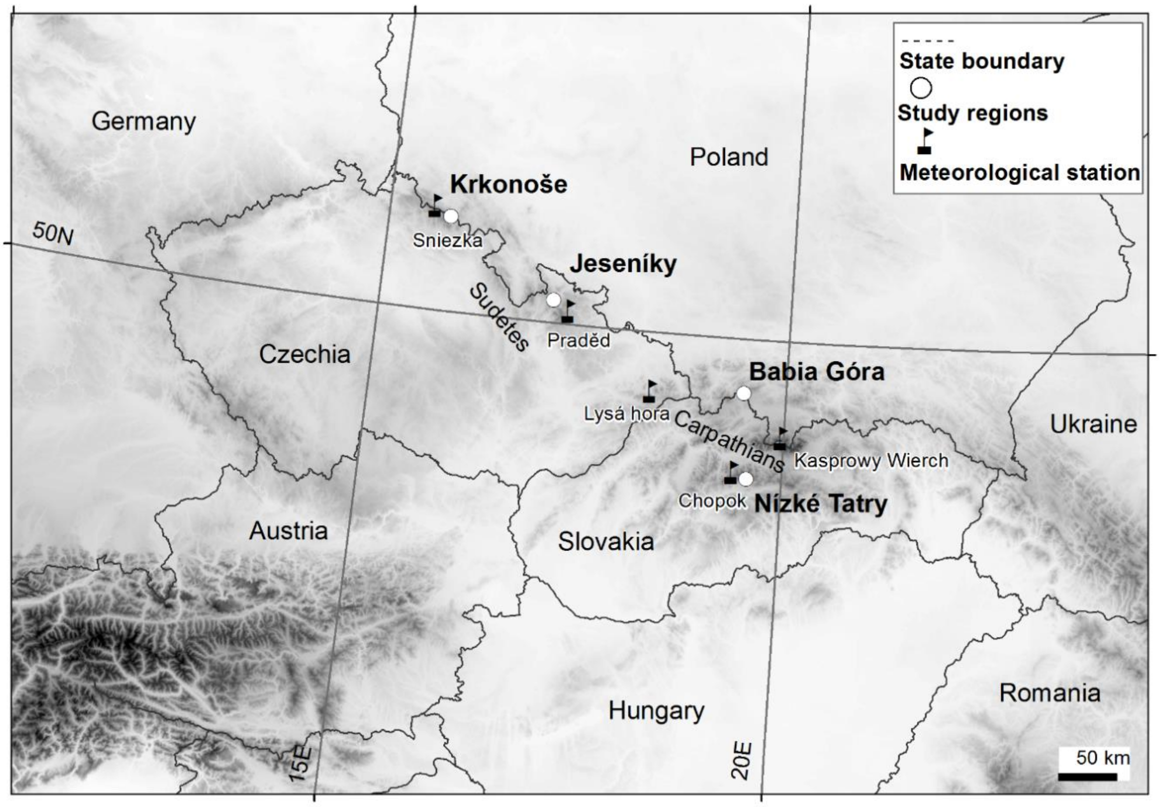

Table 1: Basic characteristics of each mountain range studied

Mountain range	Highest peak elevation (m a.s.l.)	Published average timberline elevation (m a.s.l.)*	Highest tree-group position (m a.s.l.)	June-September mean temperature (°C)
Krkonoše Mts.	1603	1340 (Treml, Migoń 2015)	1508 (Kašpar, Treml 2016)	7.7 (Kašpar, Treml 2016)
Jeseníky Mts.	1491	1405 (Treml, Migoń 2015)	1478 (Kašpar, Treml 2016)	8.3 (Kašpar, Treml 2016)
Babia Góra Mts.	1725	1370 (Czajka et al. 2015)	1679 (Kašpar, Treml 2016)	8.5 (Kašpar, Treml 2016)
Nízké Tatry Mts.	2043	1550 (Plesník 1999)	1777 (Kašpar, Treml 2016)	7.2 (Kašpar, Treml 2016)

* Average timberline elevations were derived using different methodologies.

Sampling strategy and data processing

Altogether, increment cores from total 1391 living Norway spruce from 82 sites were used in all presented analysis. In addition, 35 increment cores or cross-sections were collected and analysed from spruce construction timber from mountain huts situated above 1000 m a.s.l. in the Krkonoše Mts. Both datasets partially overlapped.

Two cores per tree were taken at breast height (app. 1.3 m above the ground) to avoid the eccentricity and compression wood due to slope inclination and prevailing wind direction. All sites were selected to represent stands with diverse age structure and without visible recent human intervention (e.g., no evidence of recent logging or grazing), however, at low-elevation sites, planted stands were also sampled. Most sampled stands were located in the vicinity of treeline ecotone, with an exception of the study nr. 3 for which three elevation belts below timberline were sampled as well (Table 2).

Cores were prepared using standard dendrochronological methods (Stokes, Smiley 1996): cores were fixed on wooden supports and sanded, and tree-ring width (TRW) was measured to the nearest 0.01 mm with a TimeTable measuring device (Vienna Institute for Archaeological Science). Successfully cross-dated series were included in the final datasets.

Tree ring series contain different short- and long-term trends caused by environmental conditions and internal tree properties such as age (Fritts 1976). Therefore, a systematic trend attributed to change in tree age and size was removed trough standardization procedure into the site chronologies (Fritts 1976).

Depending on purpose, tree ring width series were detrended using negative exponential curve spline function or regional curve standardization to remove non-climatic noise (e.g. Fritts 1976; Holmes et al. 1986; Cook and Pederson 2011). We attempted to preserve (at least) medium-frequency variability in tree-ring widths, therefore signal-free standard chronologies were created (Melvin, Briffa 2008). To preserve low- to medium-frequency growth variability, basal area increment chronologies were also built (Biondi, Qeadan 2008; Hartl-Meier et al. 2014a). All chronologies types were truncated at a minimum sample replication of at least five series.

In order to determine internal signal strength of the chronologies, different tree ring statistics were calculated, e.g. average tree ring age, mean sensitivity, 1st order autocorrelation, standard deviation, Expressed Population Signal (EPS) (Wigley, Briffa, Jones 1984).

Various statistical methods were employed to determine dissimilarity in tree-ring chronologies, e.g. hierarchical clustering (Ward's method). To extract main directions of variance, the principal component analysis (PCA) was applied (Lepš, Šmilauer 2003). Statistical significance of chronology trends was evaluated through Mann–Kendall test (Chatfield 2004).

Table 2: Basic characteristics of study sites

Region	Elevation belt	Elevation (m a.s.l.)	Site aspect	Average tree height (m)
Krkonoše Mts.	Treeline and timberline	1300–1390	N, NE, SW, SE	5–9
	Timberline-100	1200	NW, N, SE	14
	Timberline-200	1100	NW, N, SE	18
	Timberline-400	900	NW, N, SE	21
Jeseníky Mts.	Treeline and	1350–1420	N, NE, S, SW	5–10

	timberline			
	Timberline-100	1200	S, NE, NE, SW	17
	Timberline-200	1100	S, NE, NE, SW	22
	Timberline-400	900	S, NE, NE, SW	23
Babia Góra Mts.	Timberline	1450	S, SW, W	11
	Timberline-100	1350	S, SW, N, NW	18
	Timberline-200	1200	S, SW, N, NW	22
	Timberline-400	900	S, SW, N, NW	24
Nízké Tatry Mts.*	Timberline	1450	S, W	11

* Samples were also collected in elevation belt timberline-100, timberline-200, timberline-400, however they have not been used yet.

Climate data and growth-climate relationship

Climatic variables – temperature and precipitation – were used in monthly resolution. According to the purpose and with respect to the length of time series, climatic data from meteorological stations or gridded climate database were used. For the Krkonoše Mts., data were obtained from the Sniezka meteorological station (located at 1613 m a.s.l., WMO 12510) (Głowicki 1997; (Migała, Urban, Tomczy 2016). For the Jeseníky Mts. climate data were available from local station Mt. Praděd (1491 m a.s.l.). Meteorological stations Lysá hora (1322 m a.s.l., WMO 11787) and Kasprowy wierch (WMO 12650, 1989 m a.s.l.) were indicative for the Babia Góra Mts. Chopok meteorological station (WMO 11916, 2007 m a.s.l.) was used for the Nízké Tatry Mts. (Figure 1).

However, local station data covered only limited period. Therefore, the gridded CRU TS dataset (Mitchell, Jones 2005; Harris et al. 2014) which covers the period from 1901 onwards were also used.

Growth-climate relationship has been analysed according to the research goals. Basically, monthly and seasonal mean temperature and precipitation records of the previous and current year were correlated against TRW chronologies. Stability of the growth-climate relationship was assessed using moving correlation analysis. For temperature reconstruction, scaling and transfer regression function were used (Esper et al. 2005).

Residual variability of tree growth (i.e. variability not explained by climate) was further correlated with modelled sulfur and nitrogen loads. In most analyses, we pay attention to behaviour of growth-climate relations considering either high- and low-frequency components of time series.

Main results

Individual chapters represent scientific papers (Table 3) that were processed successively with respect to the main goals and the progress of field and lab works.

To sum up, all studies employ dendroclimatic methodological approach and each study extended the sample size and study sites with respect to the main goals.

In the first paper, growth pattern and growth-climate response of Norway spruce are presented to describe tree stands in the alpine treeline ecotone between 1260 m a.s.l. and 1430 m a.s.l., in opposite south- and north facing slopes in the Krkonoše Mts. and the Jeseníky Mts.

The summer temperature reconstruction and long-term growth variation of Norway spruce stands located between 1150 m a.s.l. and 1350 m a.s.l from the Krkonoše Mts. and the Jeseníky Mts. back to 1700 AD is introduced in the second paper.

The third paper deals with differences in growth-climate response along elevation gradient within the natural distribution range of Norway spruce. Samples come from four elevation belts between 900 m a.s.l. and 1450 m a.s.l. in the Krkonoše Mts., the Jeseníky Mts. and the Babia Góra Mts.

The divergence between the tree growth and summer temperature at timberlines in the Krkonoše Mts., the Jeseníky Mts., the Babia Góra Mts. and the Nízké Tatry Mts. is analysed in the fourth study.

Table 3: Main chapters of dissertation represented by individual scientific papers

Study Nr.	Full reference	Impact factor	Author´s share (%)
1	Treml, V,, Ponocná, T., Büntgen, U. (2012): Growth trends and temperature responses of high-elevation Norway spruce (Picea abies (L.) H.Karst.) in the Czech Sudetes Mountains. Climate Research, 55, 91–103. doi: 10.3354/cr01122	2.496	40
2	Treml, V., Ponocná, T., King, G. M., Büntgen, U. (2015): A new tree-ring-based summer temperature reconstruction over the last three centuries for east-central Europe. International Journal of Climatology, 35, 3160–3171. doi: 10.1002/joc.4201	3.609	40
3	Ponocná, T., Spyt, B., Kaczka, R., Büntgen, U., Treml, V. (2016): Growth trends and climate responses of Norway spruce along elevational gradients in East-Central Europe. Trees, 30, 1633–1646. doi 10.1007/s00468-016-1396-3	1.706	60
4	Ponocná, T., Chuman, T., Rydval, M., Urban, G., Migała, K., Treml, V. (2017): Divergence of tree growth and summer temperature at treelines in the East-Central Europe. Agricultural and Forest Meteorology. In rev.	4.461	60

Growth trends and temperature responses of treeline Norway spruce in the Czech-Polish Sudetes Mountains

Norway spruce growth patterns and climate response along the alpine treeline ecotone in the Sudetes Mts. were assessed with respect to aspect of the selected sites (north/south-facing) and according to their position in either the lower (timberline) or upper (treeline) part of the ecotone between 1260 m and 1430 m a.s.l.

Growth trends were analysed using non-indexed (raw) TRWs by averaging TRWs from trees with the same age. Growth-climate response was conducted employing simple Pearson correlation between TRW chronologies and monthly temperature records over their common period of overlap 1960–2006. Stability of correlation was analysed by 21 year moving window for selected seasonal periods.

Almost all chronologies shared one growth peak from 1940 to 1960 and another after the 1990s, separated by a growth depression in the 1970s and 1980s. The youngest tree rings (age ≤20) were highly variable in growth trends, unlike the TRWs of greater cambial age. In all age classes and in both regions, tree rings from timberline stands were significantly wider than those from treeline sites. Aspect-related differences in TRW were generally weak, but more pronounced in timberline stands and at higher cambial ages.

The considerable growth depression in the 1980s was more pronounced at the timberline sites and in the Krkonoše Mts., as shown by the relatively greater reduction in TRW. All age classes have shown significant increases of increments since the 1990s. The maximum TRWs for each of the study sites were achieved at the end of this period (2000 to 2007).

Indexed TRWs from timberline sites were mainly positively correlated with growing season temperatures (individual months May-July, means of May-August, May-July, or June-July). The correlation coefficients were slightly higher in the Hrubý Jeseník Mts.; their maximum values ranged from 0.41 to 0.48 at the Hrubý Jeseník Mts. sites and from 0.38 to 0.47 in the Krkonoše Mts. In addition to growing season temperatures, trees in both regions also responded positively to the temperatures of the preceding autumn and negatively to the temperatures of the preceding summer.

Indexed TRWs of trees growing on south-facing slopes in the Hrubý Jeseník Mts. were positively correlated with April temperatures, whereas those in the Krkonoše Mts. revealed positive responses to May temperatures. In the Krkonoše Mts., correlations with the peak growing season (June-August) temperature were stronger on south- facing slopes than on north-facing slopes. Generally, treeline trees were less sensitive to temperatures in both regions than those from timberline sites. Moreover, overall pattern of temperature response of treeline sites was characterized by a later maximum response, in July.

The basic trends in moving correlation coefficients comprised decreasing sensitivity of TRW to temperatures of the preceding October, and, in contrast, increasing responses to May temperatures. Correlations with growing season temperatures were relatively stationary.

Regarding the effect of the slope aspect on tree growth in the treeline ecotone only small differences in the tree ring widths were found. Small altitudinal differences seem to have consistently greater effect on the tree growth than differences in slope aspect. Weak exposure effect within the high-elevation locations could be related to strong winds preventing the radiative warming of air near the ground and therefore eliminating the advantage of south-facing slopes.

A new tree-ring-based summer temperature reconstruction over the last three centuries for east-central Europe

Master tree-ring chronology spanning the period between 1609 and 2010 was compiled using high-elevation Norway spruce tree-ring series from Sudetes (Krkonoše Mts., Králický Sněžník Mts. and Hrubý Jeseník Mts.). Both living and historical construction timber was used. Master chronology was subsequently used to reconstruct summer temperature.

Based on the strongest growth-climate response as evidenced by correlation between TRW and monthly temperatures, the mean temperature of June and July for the Sudetes Mts. was selected for the reconstruction.

To preserve temperature amplitudes and variability, a scaling approach was undertaken. Two temperature reconstructions were derived – an RCS-based reconstruction (STR-RCS) and an individual detrending-based reconstruction (STR-IND). The uncertainty attributable to detrending approach ranges from 1.2 °C (STR-IND) to 0.90 °C (STR-RCS). Uncertainty buffer is further extended by root-mean-square error 0.67 °C, which is the average value for all calibration-verification trials. As expected, the RCS-based reconstruction reveals more low-frequency variability than the individual-based detrending temperature reconstruction. Reconstructions show two pronounced periods of increased temperatures: at the turn of the 18th and 19th centuries (1787–1797 +1.9 °C anomaly by STR-IND) and between 1870 and 1880 (1873–1883 +1.3 °C anomaly by STR-RCS). Both tree rings and instrumental data confirmed that the 1950s and the last 10 years (after 2000) belonged to warmest periods. The warmest years according to the reconstruction were 1794 (+3.0 °C anomaly identified by STR-RCS and +3.4 °C anomaly by STR-IND), 1798, 1881, 1946, 2002 and 2006 (+3.8 °C; the last three are based on instrumental data). Periods of low temperatures occurred mainly in the early part of the reconstructed time series (1700–1710, −3.5 °C anomaly by STR-RCS), between 1737 and 1747 (−2.3 °C anomaly by STR-IND), between 1816 and 1826 (−1.7; −2.1 °C anomaly by STR-IND and STR-RCS, respectively) and, based on instrumental data, in the 1970s and 1980s. The lowest reconstructed June-July temperatures occur in 1744 (−4.7 °C anomaly identified by STR-RCS and −4.1 °C by STR-IND) and in 1821 (−4.0 °C by both STR-RCS and STR-IND).

The spatial signature of the Sudetes chronology mainly encompasses the areas of the Czech Republic, Slovakia, south Poland, east Austria and Hungary. In the late part of the study period (1956–2009), the area with the highest correlations shifts eastward.

Alpine reconstructions (Büntgen et al. 2011, 2009) and the reconstruction for Czech Lands based on wheat harvest (Možný, Brázdil, Dobrovolný 2012) agree more with the Sudetes temperature reconstruction than with Carpathian reconstructions (Popa, Kern 2009; Büntgen et al. 2013). The similarity between the Sudetes and Alpine or between Czech wheat harvest reconstructions is larger in the low-frequency domain. Carpathian and Central Europe (Dobrovolný et al. 2010) reconstructions, by contrast, are closer to those of the Sudetes in the high-frequency domain. The most stable moving correlations found were with the Alpine reconstruction (Büntgen et al. 2009) time series; these correlations were mostly statistically significant. From 1760 onwards, the correlations with the Central Europe reconstruction (Dobrovolný et al. 2010) are also relatively stable and significant. The moving correlations with other temperature reconstructions are rather weak or unstable.

This study emphasized the need for the new independent regional climate reconstructions based on different proxies and capturing the full range of past climatic variability.

Growth trends and climate responses of Norway spruce along elevational gradients in East-Central Europe

Growth trends and climate responses of Norway spruce within its natural elevational distribution range in the mountain regions of East-Central Europe (the Sudetes Mts. and the Babia Góra Mts.) were evaluated.

For each elevation belt (timberline, timberline-100 m, timberline-200 m, timberline-400 m) response functions were calculated between residual chronologies and monthly climatic variables over the period of common data overlap (from 1906 to 2010). In addition, moving response functions were computed over a 68-year window, which was the shortest possible window, when using two climatic variables.

Age representation was fairly equal – age classes from 70 to 180 years were represented in all chronologies. The lowest elevation belts tended to be represented by younger trees than the upper elevation belts (in the Babia Góra Mts. and the Krkonoše Mts.). In the Jeseníky Mts., both timberline trees and trees from the lowest elevation belt were younger than trees from the medium elevation belts. In all regions, TRW decreased with increasing elevation. TRWs were consistently different between timberline trees and the two lowest belts.

Residual TRWs chronologies were clustered into two main groups. The first consisted of all the lowest elevation belts and the timberline-200 m belt from Babia Góra; the other consisted of the sites situated in higher elevations. The second group was divided into two further groups: chronologies from the Krkonoše Mts., and chronologies from the Jeseníky and the Babia Góra Mts.

In the Jeseníky and the Babia Góra Mts. the timberline and lowermost elevation belt chronologies revealed two trend breakpoints, the remaining elevation belts had only one trend breakpoint. For all chronologies, the first trend breakpoint was detected between 1925 and 1933. The second was detected in 1972 or 1973 in the Jeseníky and the Babia Góra Mts., and in 1978 and 1979 in the Krkonoše Mts. and lowermost elevation belts of the remaining areas. Slopes of linear trends over fixed 30 year intervals approximating sections between main depressions and culminations were statistically significant only at timberline. In the last interval (1980–2010), increasing slopes of all chronologies were significant with the exception of the lowermost elevation belt of Babia Góra. In contrast to the Jeseníky Mts. and the Babia Góra Mts., growth depression in the 1970s was pronounced at each altitudinal level in the Krkonoše Mts.

Correlations of TRW with seasonal temperature means were highest in the elevation belt of timberline and timberline-100 m and radial growth responded primarily to June and July temperatures. June temperature loadings increased towards the east. Timberline-400 m chronologies did not display any significant response to June and July temperatures, and the response of the timberline-200 m chronology from the Babia Góra Mts. was related only to July temperature. Aside from summer temperatures, tree growth in the three highest elevational belts was significantly affected by temperature of the preceding October, particularly in the Krkonoše Mts. and the Jeseníky Mts.

The effect of precipitation on tree growth has been also analysed. The response of radial growth to summer precipitation was significant at the lowest zone (the Jeseníky Mts., the Babia Góra Mts.) or the timberline-200 m belt (the Krkonoše Mts.). Regardless of elevational position, tree growth was positively influenced by February precipitation.

Moving response function in the Krkonoše Mts. indicated that the effect of preceding October temperatures on radial growth decreased and was significant only in the first half of the study period (till 1985) in nearly all elevation belts. In addition, the response to early spring temperatures gradually transitioned from negative to positive.

In the Jeseníky Mts., there was an increasing effect of March precipitation in the timberline-100 m and timberline-200 m belts. The three elevational belts from timberline-200 to timberline exhibited obvious trends of increasing responses to summer precipitation and early spring temperature in the second half of the 20th century. In the same period, the effect of the preceding October temperatures became insignificant in the timberline zone.

In the Babia Góra Mts., tree growth responded positively to April temperatures after the 1950s–1960s except in the lowermost zone, where TRW response to April temperatures was stable and strong across time. In contrast, the positive effect of preceding October temperatures gradually diminished in the same period (timberline-100 m). In the lowermost zone of the Babia Góra Mts., the negative effect of September temperatures in the year preceding ring formation emerged during the last 40 years. Response functions of remaining monthly climatic variables either were not significant over the study period or did not show any trend.

To conclude not only different but also instable growth trends and climate responses of Norway spruce were determined along altitudinal gradient. Medium-frequency growth variability increased with elevation. The amount of explained variability within a given elevation zone increased towards the east. It was also found that trees from lower-montane zone gradually increased their sensitivity to drought.

Divergence of tree growth and summer temperature at treelines in the East-Central Europe

Norway spruce radial growth divergence from summer temperatures in mountain regions of Central Europe (the Sudetes Mts., the Babia Góra Mts., the Nízké Tatry Mts.) was explored. Growth-climate coherency was studied at timberline using tree ring chronologies of similar age structure in all sites. Two different standardization procedures were carried out in order to preserve medium to low-frequency variability in radial growth. First, signal free chronologies and secondly, basal area increment chronologies were created. Coherence in growth trends among individual TRW series within each region was inspected using inter-series correlations with a moving window of 21 years length and a 1-year step. Both correlations of TRW and June-July temperature series and correlations of TRW residuals (i.e. deviations of TRW from expected growth according to June-July temperature) with sulfur and nitrogen deposition were computed.

All signal free and basal area increment chronologies are characterized by two pronounced growth peaks. The first occurs in the 1940s–1960s, the second in the 2000s. Whereas in signal free chronologies from the Babia Góra Mts., the Nízké Tatry Mts. and the Krkonoše Mts. the first peak is rounded and culminates at the turn of the 1950s and 1960s, the Jeseníky Mts. and the Krkonoše Mts. basal area increment chronologies culminate in the late 1940s and then decrease. The prominent growth depression in the 1970s and 1980s was common to all chronologies, with its lowest point in the early 1980s. The two culmination points of the signal free TRW chronologies achieved in the 1940s and 2000s have approximately the same values. Basal area increment chronologies displayed maximum growth in the 2000s (Jeseníky Mts., Babia Góra Mts, a Nízké Tatry Mts.) with the exception of the Krkkonoše Mts. basal area increment chronology, which exhibited a maximum growth point in the 1940s.

Within the treeline chronologies the increase in growth coherency were observed in the 1930s (all regions except the Nízké Tatry Mts.) and 1970s (all regions). The period around 1930s achieved the highest correlations between TRW and June-July temperature. Growth coherency decreased in 1950s but subsequently in 1970s and 1980s coherent growth patterns rose and after 1990s remained still high.

Correlations between unfiltered TRW residuals and sulfur and nitrogen deposition were highest and significant for the Jeseníky Mts. and the Babia Góra Mts. Basal area increment residuals for the Krkonoše Mts. were also significantly correlated with nitrogen deposition. The remaining relationships were not statistically significant. In the low-frequency domain, TRW residuals were significantly correlated with both nitrogen and sulfur deposition for the Jeseníky Mts. chronologies. Nitrogen deposition was also significantly correlated with TRW residuals of signal free chronologies of the Nízké Tatry Mts. and basal area increment chronologies for Babia Góra Mts.

Our study proposes possible causes of growth divergence from summer temperature of treeline Norway spruce in East-Central Europe. We suggest that in further studies employing linear transfer functions between temperature and TRW (a typical approach to climate reconstruction, Fritts 1976), the calibration period should be long enough to capture periods with positive and negative departures of TRW from the driving climatic variable. Otherwise, prevalence of positive or negative residuals in the calibration period might distort the resulting reconstructions. These results highlight the need for recognition of non-stationary noise in relation between temperature and tree growth which is attributed not only to anthropogenic pollution but also to changes in seasonal window of tree growth sensitivity to climate.

Conclusions

The growth-climate relationships of Norway spruce have been studied along a 600 km longitudinal transect in East-Central Europe. Main tasks of the dissertation have been resolved in four independent studies.

On the example of treeline ecotone in the Krkonoše and the Hrubý Jeseník Mts., we found that elevation-driven radial growth variability is substantially higher than aspect-driven variability. Weak exposure effects within the high-elevation locations could be related to regional-scale effects, especially to strong winds preventing heating of air near the ground and therefore eliminating the advantage of south-facing slopes. All studied sites from treeline ecotone reveal a close relationship between ring widths and growing season temperatures. Trees located at the upper boundary of the treeline ecotone reacted positively to preceding autumn temperatures, and their temperature response was slightly weaker than that of trees from the upper forest limit. Temporal trends in growth−climate responses consisted mainly of a gradual decrease in the influence of preceding October temperatures and an increasing effect of May temperatures towards the present. The proportion of younger trees generally increases upwards within the ecotone, and the most recent growth rates appear unprecedented in a century-long context suggesting recent upward advance of treeline ecotone.

However, at four timberlines in east-central Europe (the Krkonoše Mts., the Hrubý Jeseník Mts., the Babia Góra Mts., the Nízké Tatry Mts.) we found that the relation between radial growth and June-July temperature (as the most important climatic driver of growth) has not been stable and tree-ring widths diverged from the course of June-July temperatures in some periods. It seems that the acid pollution in 1970s and 1980s was important but not the only one reason for varying divergences of TRW from summer temperature in the 20th century and recently. We propose that departures of tree growth could be caused by (i) changing time-window of TRW sensitivity to climate and (ii) by a pollution load. The changing time-window included especially prevailing strong responses of TRW to July temperature in long growing seasons and the predominant importance of June temperatures during short growing seasons (with cell division and enlargement constrained to a shorter period).

Extensive data set of Norway spruce temperature-sensitive tree-ring series allowed us to create a new temperature reconstruction of June-July temperature. The present temperature reconstruction for the Sudetes and east-central Europe records temperature variations spanning back to 1700. It provides evidence that mountain ecosystems in this region have experienced summer temperature fluctuations with 4.2 to 4.8 °C amplitudes between the coldest and warmest decades. The coldest period was the beginning of the 18th century, and the warmest periods were the 1790s and the last decade (2000–2009). Whereas the coldest periods were about −3.5 to −2.3°C cooler, the warmest period was 1.3 to 1.9°C warmer than reference period 1961–1990, with above mentioned ranges arising from different standardization procedures. A comparison with other reconstructions derived from documentary archives and from tree rings indicates that tree-ring-based temperature reconstructions are able to preserve more low-frequency variability than reconstructions based on indexed descriptions of weather inferred from documentary sources. The ability to preserve more low-frequency variability together with possible differences in temperature trends attributed to altitude and intrinsic properties of tree-ring data may lead to higher coherence between more distant high-elevation tree-ring reconstructions compared to regionally closer reconstructions based on lowland documentary data.

To resolve the question whether there is variability in growth trends and climate responses along elevation gradient in montane forest or not, we compare the growth patterns of Norway spruce in elevation belt capturing 400 m vertical zone from timberline downwards. While temperature-limited trees in the upper montane zone adjacent to timberline exhibited high medium-frequency growth variability and a strong increasing growth trend since the 1980s, trees in the lower-montane zone (400 m below timberline) displayed relatively low medium-frequency variability and a stable or slight decreasing growth trend in the last decade. The transition between temperature-limited trees and trees of mixed climate sensitivity was found to increase in elevation towards the east, which further corresponded to an increase in timberline position. Trees in the lower montane zone tended to be more affected by drought in recent decades than before. Ongoing warming likely results in increasing radial growth rates of the Norway spruce forests adjacent to timberline, whereas the productivity of lower montane forests will exhibit ambiguous trend or even decline.

This dissertation thesis represents the first comprehensive study of the tree growth response to changing climate at treelines and montane forests of East-Central Europe. It could by sum up that in treeline ecotone the radial growth variability driven by elevation is substantially higher than aspect-driven variability. Temporal trends in growth-climate responses have consisted mainly of a gradual weakening of the importance of the influence of preceding October temperatures and an increasing effect of spring temperatures towards the present. The relation between radial growth and June-July temperature as the most important climatic driver of Norway spruce growth has not been stable. This instability was influenced particularly by a changing seasonal window of growth sensitivity to temperature and by the effect of acid pollution. Nevertheless, our extensive data set allowed reconstruction of summer temperatures back to 1700. This reconstruction captures the full range of past variability and fills spatial gap in large-scale dendroclimatic network in Europe.

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Growth trends and temperature responses of treeline Norway spruce in the Czech-Polish Sudetes Mountains

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ABSTRACT: The Earth's climate system has recently experienced substantial warming, and associated effects are often most pronounced at species-specific distribution limits. Treeline ecotones may therefore be particularly useful to assess the complex interplay of biotic and abiotic factors in relation to environmental change. Here, we present site-dependent growth trends and climate responses of 22 Norway spruce *Picea abies* (L.) H. Karst. tree-ring chronologies from the treeline ecotone in the Sudetes Mountains (Mts.) along the Czech-Polish border. Annually resolved and absolutely dated ring-width measurements from 2 regions (Giant Mts. and Hrubý Jeseník Mts.), separated by aspect and altitude, resulted in robust chronologies for the 20th century. All sites reveal a close relationship between ring widths and growing season temperatures. The main site-dependent differences in growth trends and temperature responses were attributed to altitude. Trees located at the upper boundary of the treeline ecotone reacted positively to preceding autumn temperatures, and their temperature response was slightly weaker than that of trees from the upper forest limit. Temporal trends in growth–climate responses consisted mainly of a gradual decrease in the influence of preceding October temperatures and an increasing effect of May temperatures towards the present. The proportion of younger trees generally increases upwards within the ecotone, and the most recent growth rates appear unprecedented in a century-long context.

KEY WORDS: Czech Republic · Dendrochronology · Norway spruce · Sudetes Mountains · Temperature response · Treeline · Tree rings

1. INTRODUCTION

Ongoing climate change likely impacts the diversity and productivity of many ecosystems at various spatiotemporal scales (e.g. Stenseth et al. 2002). Temperature-limited communities close to their distributional margins are especially vulnerable to any alteration of the heat balance, in terms of both long-term temperature trends and their superimposed extremes (Lenoir et al. 2008). The alpine treeline ecotone is among the most prominent temperature-driven ecological phenomena (Körner 2007). This biogeographic boundary relies mainly on decreasing temperature with increasing altitude, characterized by an associated decline in the tree life form, for which both the sink (or growth) limitation and source (photosynthesis, nutrients) limitation hypotheses have been offered as explanations (Körner 1998).

Contemporary responses of treeline trees to climate change may differ due to regional variations in climate and the influence of local (non-altitudinal) factors including topography, competition, frequency

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of disturbances, summit effects, and anthropogenic impacts (Körner 1998, Holtmeier & Broll 2007, Harsch et al. 2009). One of the most important non-altitudinal treeline drivers is the large, topography-induced variability in near-ground temperatures (Körner 2007). Since the alpine treeline ecotone is especially sensitive to changes in available heat, it may also react to such topography-induced temperature alternations.

Until now, growth–climate response patterns have frequently been studied in high-elevation forest zones, where the formation of tree rings is strongly related to changes in growing season temperature, and the effect of precipitation is generally of secondary order (Fritts 1976). Central European Norway spruce *Picea abies* (L.) Karst. ring-width chronologies from high-elevation stands have recently been examined for potential relationships with climate over space and time, mainly in the European Alps (Rolland et al. 1998, Frank & Esper 2005, Büntgen et al. 2006, 2008) and the Western Carpathians (Bednarz et al. 1999, Savva et al. 2006, Büntgen et al. 2007). A few studies have reported that the reactions of trees to individual climatic variables differ along the treeline ecotone, suggesting that the effects of these drivers are influenced by climatic stress intensity (Oberhuber 2004, Vittoz et al. 2008, Leonelli et al. 2009, Moser et al. 2010).

Less attention has been paid to possible growth–climate interactions related to differing slope aspects and stand positions within complex ecotone settings outside the main alpine mountain systems. In fact, the common type of mountains with fully developed forest-tundra ecotones also consists of geologically old (e.g. Hercynian, Caledonian) mountain chains with treelines close to summits on less inclined slopes. The topography-induced microclimate in such mountains often differs from true alpine mountain ranges.

Here, we assessed patterns of spruce growth trends and their climate responses along the alpine treeline ecotone in the Sudetes Mountains (Mts.). Sampling sites were selected based on their aspect (north/south facing) and according to their position in

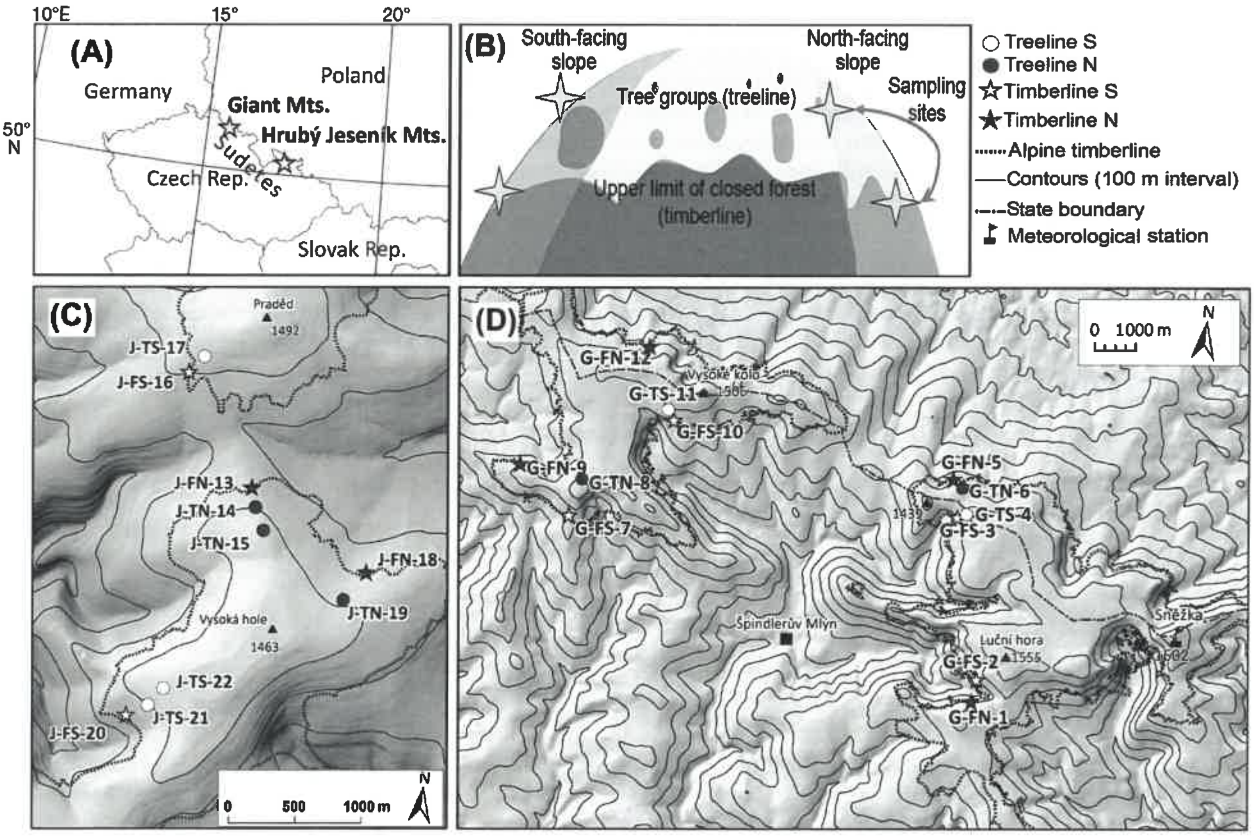

Fig. 1. Geographical position of study areas and sample plots. (A) Study areas in Europe. (B) Configuration of study sites, where shading shows regions of a given slope aspect, timberline, and treeline. (C) Hrubý Jeseník Mountains. (D) Giant Mountains. Site codes are designed as follows: study area (G: Giant Mts., J: Hrubý Jeseník Mts.); site position (T: treeline, F: upper forest limit); aspect (N: north, S: south); site number (1–22)

either the lower (timberline) or upper (treeline) part of the ecotone between 1260 and 1430 m a.s.l. We hypothesized that even small, site-dependent differences in microclimate may result in significant differences in growth responses to temperature means, potentially even defining the seasonality of the responses.

2. MATERIALS AND METHODS

2.1. Study area

The Giant Mts. and Hrubý Jeseník Mts. are the highest parts of the Sudetes mountain chain, which stretches along the Czech and Polish border (Figs. 1 & 2). Acid crystalline rocks characterize both ranges. Their relief consists of high-elevation, gently sloping surfaces dissected by deep valleys. Several peaks in the Giant Mts. surpass 1500 m a.s.l., with the highest elevation, Mt. Snezka, reaching 1602 m a.s.l. The Hrubý Jeseník Mts. are generally lower, with the highest peak being Mt. Praděd (1491 m a.s.l.). Over the period 1961 to 1990, the annual average air temperature near the upper forest limit (1300 m a.s.l.) was 2.1°C (Květoň 2001). The study area is characterized by relatively high amounts of total annual precipitation (from 1400 mm in the Hrubý Jeseník Mts. to 1600 mm in the Giant Mts.), with a significant percentage falling as snow between November and April.

The alpine treeline, with an average altitude of 1290 m a.s.l. in the Giant Mts. and 1310 m a.s.l. in the Hrubý Jeseník Mts., extends from several tens to several hundreds of meters below the summits (Fig. 2), and is influenced by extreme, summit-associated wind conditions. The typical Sudetes treeline ecotone comprises gradually opening spruce stands at the timberline, giving way to clonal clumps of spruce and dwarf pine *Pinus mugo* Turra above it (Vacek et al. 2011). The height of the spruces at timberline is usually 8 to 9 m, with groups at the highest elevations (1450 to 1500 m a.s.l.) consisting of trees no higher than 2 m.

The extent of the forest-free area in the Sudetes has been enlarged by anthropogenic deforestation (fires, grazing). This deforestation began in early medieval times, around 1100 yr ago (Novák et al. 2010), and was most intensive during the 18th century. Direct human influence (grazing, hay making, logging), however, drastically decreased around 80 yr ago (Jeník 1961). High-elevation forests in the Sudetes also experienced acid air pollution, which resulted in marked growth depression in the 1970s and 1980s, and was most pronounced in the Giant Mts. (Sander et al. 1995).

2.2. Sampling strategy and data processing

Twenty-two sampling plots (Fig. 1 and see Table 1) (12 timberline and 10 treeline sites) were established between 2008 and 2010. Pairwise plots were positioned on north- and south-facing slopes at the same altitude in stands not obviously disturbed by human activities. All study plots were located at the upper

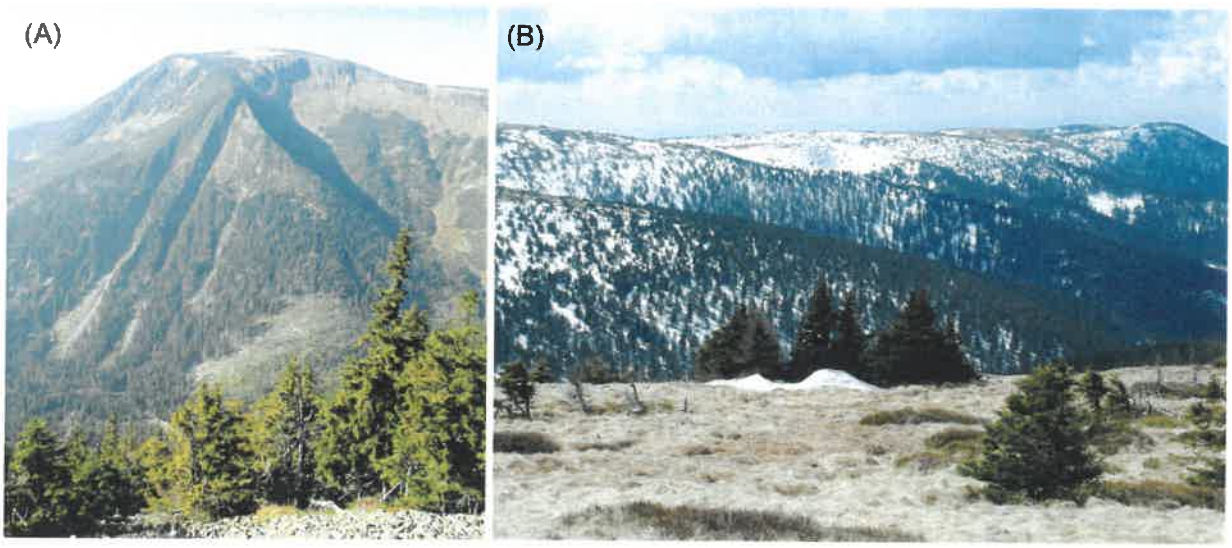

Fig. 2. Views of typical relief and treeline ecotone in the Sudetes. (A) Giant Mts. (B) Hrubý Jeseník Mts.

reaches of the timberline, mainly within the most elevated quartile of timberlines for the Giant Mts. and Hrubý Jeseník Mts. A total of 18 to 22 dominant and co-dominant spruce trees were sampled at approximately 1 m stem height in each plot. Two cores per tree were taken to avoid the dominance of compression wood due to slope inclination and wind direction.

Core samples were fixed on wooden supports and sanded, and tree-ring width (TRW) was measured to the nearest 0.01 mm with a TimeTable measuring device (Vienna Institute for Archaeological Science). For each tree, the mean TRW of both cores was used in subsequent analysis after cross-dating and missing ring identification using PAST 4 software (Knibbe 2004) and COFECHA (Holmes 1983).

Individual series were subjected to standard detrending procedures. In order to suppress heteroscedasticity, data were additionally transformed using adaptive power transformation (Cook & Peters 1997), after which cubic smoothing splines with 50% frequency cutoff at 70 yr were fitted to each series (Cook & Peters 1981). This spline length corresponds to the mean segment length. Site-specific residual chronologies were created using robust means. This method of age trend removal emphasizes interannual to multi-decadal growth fluctuations. Mean sensitivity as a measure of the relative year-to-year variability and Expressed Population Signal (EPS) were computed in order to test for internal signal strength (Wigley et al. 1984).

Hierarchical clustering (Ward's method) based on the common overlapping period (1960 to 2008) assessed coherency among the individual chronologies. Euclidean distance based on the sum of squares was used as a dissimilarity measure. Ward's method joins groups that do not exceed an acceptable level of heterogeneity, thus resulting in clusters that are as homogenous as possible (Ward 1963). Principal component analysis (PCA) was applied for the same overlapping period in order to evaluate the common signal captured in the main directions of variance (i.e. PCA axes; Lepš & Šmilauer 2003). The relationships of PCA axes to site properties were assessed using *t*-tests, with site PCA loadings as dependent variables, and regional provenance, aspect, and site position within ecotone as grouping variables.

In addition to growth variation, as revealed by indexed TRW chronologies, we also analyzed changes in the absolute growth rates both over calendar time and within each cambial age class. To increase sample sizes for comparison, cores were pooled according to site aspect and position within the ecotone. Raw TRW was tested for the influences of slope aspect, site position within the ecotone, and region each year either with the *t*-test or the Mann-Whitney *U*-test (MWU), depending on the data distribution. To reduce the effect of multiple testing, confidence levels were adjusted using the Bonferroni correction (Meloun & Militký 2006).

2.3. Growth–climate response analysis

We correlated temperature records against indexed TRW chronologies over their common period of overlap. We also assessed the stability of the growth–temperature relationships over longer periods using moving correlation analysis. Monthly resolved temperature measurements from the Giant Mts. for the years 1881 to 2006 were obtained from the Sněžka meteorological station, located at 1602 m a.s.l. (Fig. 1). The temperatures recorded by this station represent those of the upland plateau (Głowicki 1997), and the studied sites are within 2 to 12 km of this station. For the Hrubý Jeseník Mts., climate data were available from Mt. Praděd (1491 m a.s.l.). However, data from this climate station only cover the period 1946 to 1995. Therefore, we used the gridded CRU TS 3.1 dataset (Mitchell & Jones 2005) which covers the period 1901 to 2009. Correlation coefficients between the CRU TS 3.1 and Praděd station data were higher than 0.95, with the exception of the monthly temperature means for October ($r = 0.89$) and November ($r = 0.87$).

Growth–temperature relationships in the period covered by all chronologies were determined using simple correlation analysis (Pearson's correlation coefficients). The significances of correlation coefficients were tested assuming a normal distribution. The monthly and seasonal temperature means of the previous and current years were considered. The resulting site correlation coefficients were finally represented as means of sites grouped according to their position in the treeline ecotone (timberline/treeline), aspect (north/south), and region (Giant Mts./Hrubý Jeseník Mts.).

Correlations were also computed over 21 yr moving windows. Only selected seasonal periods were chosen for moving correlation analysis: the early growing season (May), peak growing season (June–July), and the preceding October. The statistical significance of monotonic decreasing or increasing trends in moving correlation coefficients was tested using the Mann-Kendall test (Hirsch et al. 1991). Standardized *Z*-statistics were used in order to detect the significance and slope of either negative or positive trends. Differences in Z-values between study regions, aspects, and site positions within the treeline ecotone were tested using the MWU test with Bonferroni correction. Trend significances were computed over the 2 periods shared by the maximum number of possible chronologies and with available climate data (1925–1996: N = 9; 1952–1996: N = 15).

3. RESULTS

3.1. Chronology characteristics

Cambial ages approximated by segment lengths of individual timberline trees most frequently ranged between 81 (Giant Mts. mean) and 92 yr (Hrubý Jeseník Mts. mean; Table 1), with this difference being statistically significant ($t = 2.51$, $p < 0.01$). Significantly shorter series originated from south-facing than from north-facing slopes (MWU $p < 0.01$, see Table 1 for details). In both regions, treeline stands were generally younger than timberline stands (treeline: mean age for Giant Mts. = 59 yr, Hrubý Jeseník Mts. = 49 yr), which was significant both when considering south- and north-facing slopes together and when comparing for the different slope aspects separately (in all cases, MWU $p < 0.01$). The most abundant series at timberline sites started between the years 1910 and 1940, whereas at treeline sites, series with the first tree-ring from between 1940 and 1960 prevailed. Populations of dominant and co-dominant trees therefore established with a ca. 20 yr lag at treeline sites.

The mean sensitivity was higher at treeline than at timberline sites (MWU $p < 0.01$), with treeline stands also being characterized by a higher amount of missing rings (MWU $p < 0.01$) (Table 1), suggesting higher climatic stress. Missing rings were more

Table 1. Basic characteristics of individual sites and respective tree-ring chronologies. Segment length indicates cambial age of tree. Site codes as in Fig. 1. TRW: tree-ring width; EPS: Expressed Population Signal

Site	Position along ecotone	Altitude (m a.s.l.)	Slope (°)	Aspect	Mean tree height (m)	No. of trees	Mean/max. segment length (yr)	Mean TRW (mm)	Mean no. of missing rings tree^{-1}	Raw series: Mean sensitivity	Raw series: 1st order auto-correlation	Standardized chronology: Mean sensitivity	Standardized chronology: EPS
G-FS-2	Timberline	1300	27	SW	8.0	19	48/64	2.20	0.15	0.250	0.662	0.212	0.95
G-FN-1	Timberline	1300	32	N	8.5	14	103/129	1.35	0.21	0.235	0.794	0.178	0.90
G-FS-3	Timberline	1320	18	SW	8.7	19	81/134	1.73	0.14	0.241	0.767	0.202	0.93
G-FN-5	Timberline	1300	21	N	8.5	16	92/142	1.65	0.47	0.218	0.827	0.155	0.89
G-FS-7	Timberline	1260	14	SW	8.1	15	69/116	1.66	0.08	0.251	0.722	0.172	0.93
G-FN-9	Timberline	1275	24	N	8.5	15	73/108	1.39	0.20	0.256	0.850	0.220	0.96
G-FS-10	Timberline	1310	14	SW	9.5	16	92/140	1.38	0.06	0.223	0.823	0.216	0.94
G-FN-12	Timberline	1290	17	NW	8.6	14	106/168	1.12	0.42	0.220	0.856	0.158	0.87
G-TS-4	Treeline	1360	13	SW	5.6	18	55/82	1.09	1.53	0.266	0.691	0.226	0.87
G-TN-6	Treeline	1360	24	N	5.2	15	64/144	0.68	1.28	0.303	0.731	0.184	0.86
G-TN-8	Treeline	1390	15	NE	4.3	17	44/61	1.37	1.04	0.303	0.599	0.202	0,90
G-TS-11	Treeline	1390	17	SW	4.3	15	70/137	0.98	1.60	0.266	0.800	0.178	0,89
J-FN-13	Timberline	1370	17	N	7.8	16	88/115	1.39	0.250	0.227	0.783	0.191	0.92
J-FS-20	Timberline	1348	19	SW	7.8	16	105/175	1.45	0.187	0.228	0.758	0.164	0.92
J-FS-16	Timberline	1402	13	S	7.6	17	95/169	1.12	0.000	0.227	0.770	0.231	0.94
J-FN-18	Timberline	1355	14	NE	7.7	18	82/166	1.28	0.056	0.218	0.760	0.206	0.94
J-TN-14	Treeline	1395	14	N	5.3	16	57/109	1.19	0.125	0.293	0.756	0.205	0.86
J-TS-21	Treeline	1400	15	SW	5.8	17	48/80	1.35	0.172	0.263	0.701	0.192	0.90
J-TS-17	Treeline	1435	12	S	5.0	17	49/91	1.19	0.235	0.294	0.687	0.213	0.91
J-TN-19	Treeline	1405	12	NE	6.3	16	47/90	1.64	0.125	0.235	0.594	0.171	0.91
J-TN-15	Treeline	1429	14	N	2.8	16	45/92	0.82	0.131	0.330	0.675	0.209	0.93
J-TS-22	Treeline	1436	11	SW	3.0	15	50/105	0.78	0.735	0.361	0.669	0.229	0.91

numerous in the Giant Mts. in comparison with Hrubý Jeseník samples (MWU $p < 0.01$). First-order autocorrelation was higher at timberline than at treeline stands (MWU $p < 0.01$), and this difference was more pronounced at Hrubý Jeseník sites. Except for the number of missing rings, no other characteristic of site chronologies was significantly affected by regional provenance or site aspect. EPS of all chronologies exceeded the 0.85 threshold of chronology robustness (Wigley et al. 1984).

As shown in Fig. 3, residual TRW chronologies were relatively similar (first PCA axis explained 68% of the variance). The second PCA axis explained 12% of the variance. Differences captured along axis 2 are attributed mainly to those between the 2 regions ($t = 14.4$, $p < 0.01$). PCA loadings on axis 3 were significantly differentiated by site position (treeline–timberline, $t = 2.78$, $p = 0.01$). However, the contribution of the third axis was small, as it explained only 5% of the overall variance. Aspect-related differences, if present, were found only at the final level of branching of the dendrogram describing similarity of individual chronologies (Fig. 4).

3.2. Growth trends

Growth trends are described using non-indexed TRWs (Fig. 5). This approach is based on averaging ring widths from trees of similar ages. It enabled us to detect site-related temporal trends in TRW without the possible bias caused by indexing. Almost all chronologies shared 1 growth peak from 1940 to 1960 and another after the 1990s, separated by a growth depression in the 1970s and 1980s. The youngest tree rings (age ≤20) were highly variable in growth trends, unlike the TRWs of greater cambial age. In all age classes and in both regions, tree rings from timberline stands were significantly wider than those from treeline sites (t-tests, $p < 0.016$). Aspect-related differences in TRW were generally weak, but more pronounced in timberline stands and at higher cambial ages. Significantly wider tree rings (MWU, $p < 0.016$) were found from south-facing than from north-facing timberline stands in 16% of cases (years) for the 21–40 yr age class, 15% of the 41–60 yr age class, and 28% of the 61–80 yr age class. An exception was noted in tree groups of the age class 41–60 yr from the Giant Mts., in which, since 2003, the highest increments were achieved on north-facing slopes. Significant regional differences in TRW were detected in about 13 to 40% of cases (years) in the case of treeline sites and from 4 to 32% of cases in timberline stands (t-tests, $p < 0.016$). Although in the 1970s and 1980s, TRWs were greater in the Hrubý Jeseník Mts., there was no clear trend for the rest of the study period.

The considerable growth depression in the 1980s was more pronounced at the timberline sites and in the Giant Mts., as shown by the relatively greater reduction in TRW. All age classes have shown significant increases of increments since the 1990s. The maximum TRWs for each of the study sites were achieved at the end of this period (2000 to 2007).

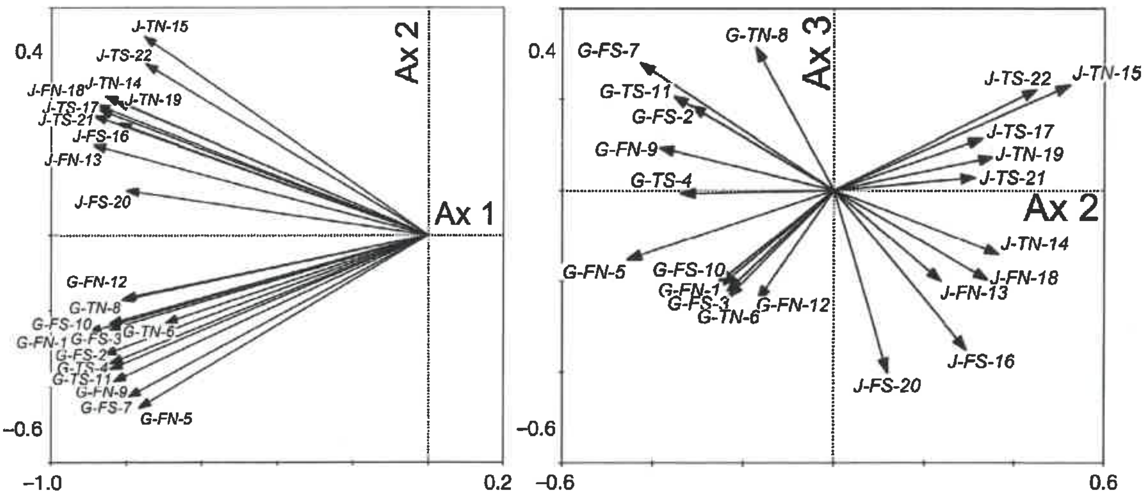

Fig. 3. *Picea abies*. Principal components (PCA) ordination scheme of Norway spruce tree-ring width (TRW) chronologies based on a common overlap period 1960–2008. (A) Axes 1 and 2, (B) Axes 2 and 3 where axes correspond to individual PCs (e.g. Ax 1 = PC1). Site codes as in Fig. 1

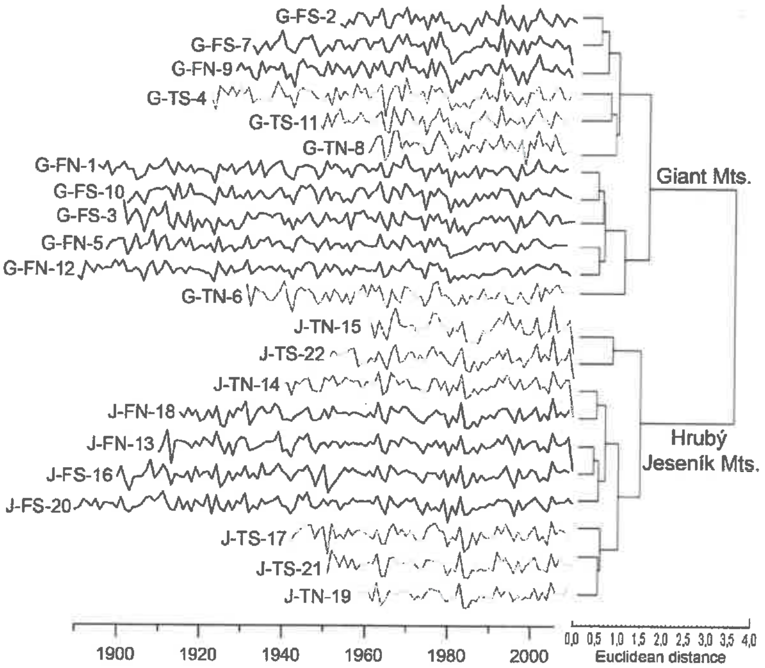

Fig. 4. *Picea abies.* Residual site chronologies (see Section 2 for more details) of treeline and timberline sites with their similarity indicated by hierarchical cluster analysis. Treeline chronologies are in gray, timberline chronologies in black. Site codes as in Fig. 1

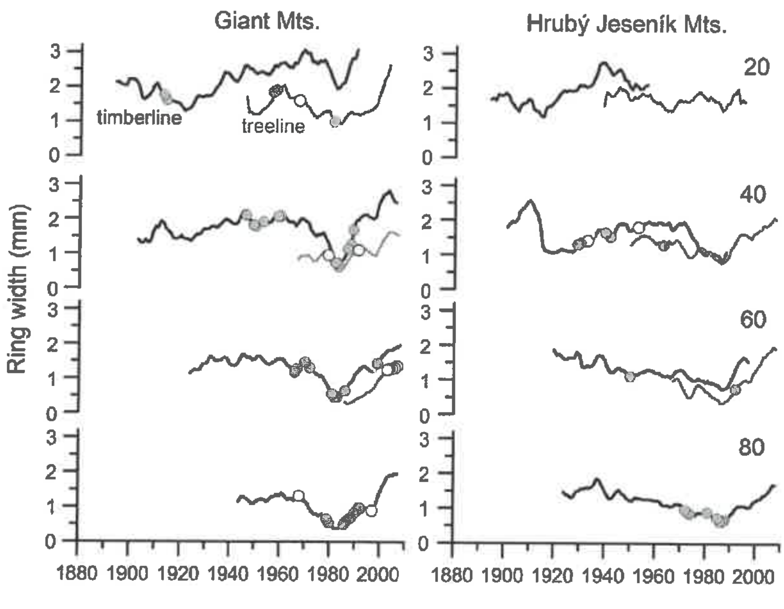

Fig. 5. *Picea abies.* 5 yr moving means of ring widths for individual age classes (cambial age classes 1–20, 21–40, 41–60 and 61–80 yr; 20, 40, 60, 80 respectively) of Norway spruce in the Giant Mts. and the Hrubý Jeseník Mts. Circles denote significant differences in tree-ring width between differing slope aspects (*t*-test, $p < 0.016$ after Bonferroni correction). Grey circles: wider tree rings on south-facing slopes; white circles: wider tree rings on north-facing slopes

3.3. Temperature responses

In the period shared by all chronologies (1960 to 2006), indexed TRWs from timberline sites were mainly positively correlated with growing season temperatures (individual months May–July, means of May–August, May–July, or June–July; Fig. 6). The correlation coefficients were slightly higher in the Hrubý Jeseník Mts.; their maximum values ranged from 0.41 to 0.48 at Hrubý Jeseník sites and from 0.38 to 0.47 in the Giant Mts. In addition to growing season temperatures, trees in both regions also responded positively to the temperatures of the preceding autumn and negatively to the temperatures of the preceding summer. Although these relations were statistically non-significant, they remained consistent among most sites. The effects of aspect on timberline tree reaction to temperatures differed between the regions. Indexed TRWs of trees growing on south-facing slopes in the Hrubý Jeseník Mts. were positively correlated with April temperatures, whereas those in the Giant Mts. revealed positive responses to May temperatures. In the Giant Mts., correlations with the peak growing season (June–August) temperature were stronger on south-facing slopes than on north-facing slopes.

Apart from site G-TN-8 ($r = 0.46$), treeline trees were less sensitive to temperatures in both regions (Giant Mts., maximum $r = 0.30$–0.36; Hrubý Jeseník Mts., maximum $r = 0.34$–0.44) than those from timberline sites. The overall pattern of temperature response of treeline sites was characterized by a later maximum response, in July. Moreover, correlations with April temperatures were far from significant, and the first month in the growing season that showed a significant positive correlation was May. Unlike those from the Hrubý Jeseník Mts., 3 of the 4 Giant Mts. treeline chronologies showed significant cor-

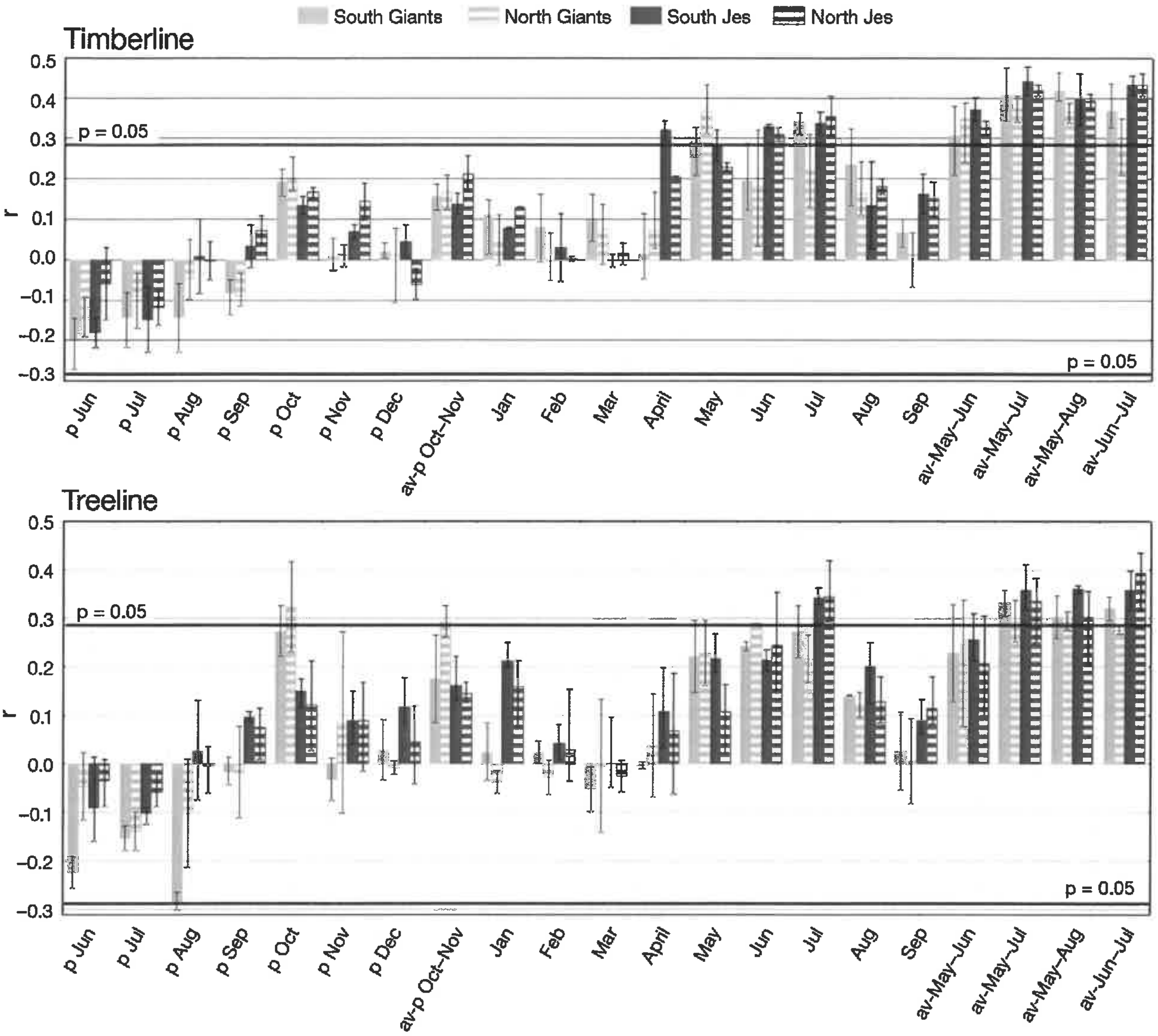

Fig. 6. *Picea abies*. Pearson correlations between temperature means and corresponding indexed tree-ring widths. Average values (columns), and maximum and minimum values (whiskers) represent all sites grouped according to aspect and region. Giants: Giant Mts.; Jes: Hrubý Jeseník Mts.; south: South-facing; north: North-facing; av: average; p: previous

relations with preceding autumn temperatures (October or the October–November mean; Fig. 6). Regarding aspect-related temperature–growth differences, both of the south-facing treeline sites in the Giant Mts. exhibited relatively strong negative responses to preceding August temperatures, whereas in the Hrubý Jeseník Mts., south-facing sites reacted positively to May temperatures.

The basic trends in moving correlation coefficients (21 yr window) comprised decreasing sensitivity of TRW to temperatures of the preceding October, and, in contrast, increasing responses to May temperatures (Fig. 7). Correlations with growing season temperatures were relatively stable. The decreasing trend of correlations with preceding October temperatures was common to almost all sites (Table 2). Trends in response to May temperatures were not homogenous, because a small number of sites did not react at all. Trends in responses both to May and to preceding October temperatures were not affected by site characteristics (region, altitude, aspect; *t*-tests, $p > 0.0016$). In contrast, trends in correlations with June–July temperatures were stratified by region (*t*-test, $p < 0.01$). While growth sensitivity to peak growing season temperatures slightly increased in the Hrubý Jeseník Mts., the opposite

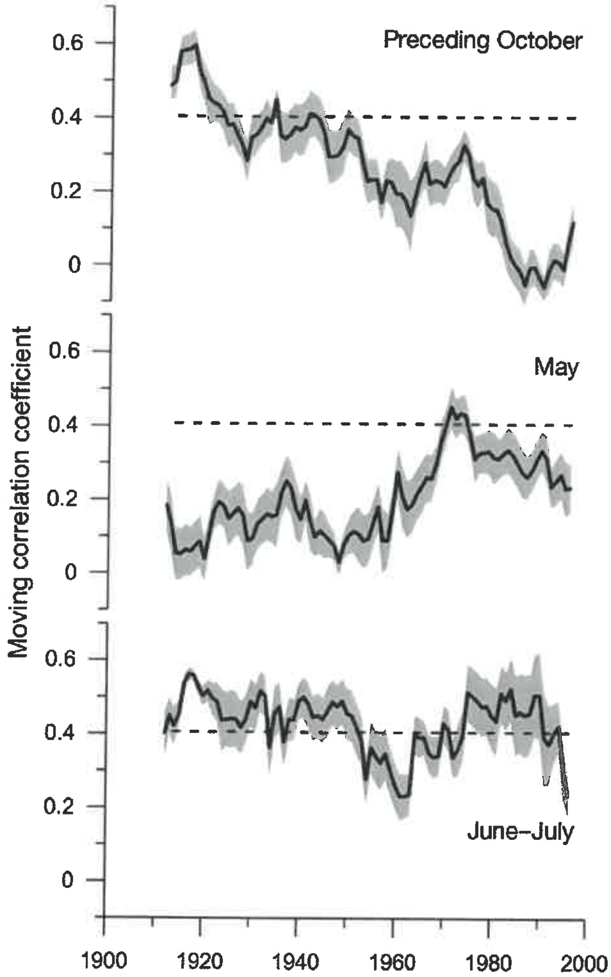

Fig. 7. *Picea abies*. 21 yr running correlations of tree-ring width indices and selected temperature means for October of the preceding autumn, May, and June–July. Average values (black) with standard deviations (grey) are plotted. Dashed line: p = 0.05

Table 2. Trend analysis for growing season temperature–growth correlations. Mann-Kendall *Z*-values and their statistical significances are given: p* ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001. Site codes as in Fig. 1

Site	Z-values		
	Preceding Oct	May	June–July
1925–1996			
G-FN-1	−3.32***	5.62***	−5.56***
G-FS-3	−6.29***	4.20***	−8.08***
G-FN-5	−8.06***	5.09***	−6.51***
G-FS-10	−4.36***	7.68***	−0.53
G-FN-12	−3.71***	1.71	−5.89***
J-FN-13	−7.21***	1.27	6.08***
J-FS-16	−7.29***	7.58***	2.42*
J-FN-18	−7.56***	6.17***	2.31*
J-FS-20	−6.83***	5.46***	5.95***
1952–1996			
G-FN-1	−3.41***	5.55***	−4.99***
G-FS-3	−6.05***	1.81	−2.63**
G-FN-5	−6.29***	3.90***	−6.82***
G-TN-6	−1.64	4.84***	−4.74***
G-FS-7	−3.88***	−0.32	0.38
G-FN-9	−5.91***	−0.71	−2.92**
G-FS-10	−3.94***	2.22*	−0.44
G-TS-11	−6.09***	0.87	4.96***
G-FN-12	−3.16**	6.11***	−3.81***
J-FN-13	−4.53***	1.63	5.25***
J-TN-14	−2.08*	5.17***	5.80***
J-FS-16	−7.21***	1.59	2.18*
J-TS-17	−3.22**	−5.44***	6.02***
J-FN-18	−2.83**	3.69***	3.92***
J-FS-20	0.24	2.67**	4.47***

trend was evident at the Giant Mts. sites. A significant drop in temperature sensitivity of most stands was detected from 1953–1965 for June–July and preceding October temperatures.

4. DISCUSSION AND CONCLUSIONS

4.1. Growth variability

Growth–temperature responses were studied at the upper distributional limits of Norway spruce in 2 areas more than 120 km apart along the Sudetes mountain chain. Despite the large distance between regions, and differences in altitudes and slope aspects among sampled stands, the resulting indexed TRW chronologies shared almost 68% of their total variance. This common variance among sites represents growth reactions to macroclimatic conditions. The remaining part of the variance was driven mainly by regional-scale effects (12%) and by site position (elevation) within the alpine treeline ecotone (5%). The least pronounced differences were attributable to site aspect (north/south). In other mountain systems, regional provenance has been shown to have the strongest clustering effect (Carrer et al. 2007). Oberhuber (2004) also reported a stronger effect of site altitude than site aspect from treeline ecotones in the inner Austrian Alps. Thus, even small altitudinal differences seem to consistently have greater effects than differing slope aspects on tree growth along the treeline ecotone. Raw TRWs revealed a similar pattern of spatial variation. In both the Giant Mts. and the Hrubý Jeseník Mts., they mainly followed altitudinal gradients along the alpine treeline ecotones, with no definite tendency in

TRW differences related to site aspect. Weak exposure effects within the high-elevation locations could be related to strong winds preventing heating of air near the ground and therefore eliminating the advantage of south-facing slopes (Treml & Banaš 2008).

We found that tree growth in the treeline ecotone of the Sudetes Mts. is governed by growing season temperatures, similarly to other high-elevation sites (Fritts 1976). In our study, the May–July temperatures drove radial growth with the greatest effect. Correlation coefficients found for the relationship between site chronologies and seasonal temperature means were similar to those from other temperature-limited sites in the Alps (Frank & Esper 2005, Büntgen et al. 2008) and Tatras (Savva et al. 2006, Büntgen et al. 2007), but were higher than those from nearby ranges below the timberline (Wilson & Hopfmueller 2001, Rybníček et al. 2009). According to a large-scale European comparison (Mäkinen et al. 2003), Norway spruce growing within the range of June–July temperatures of 8 to 10°C, as in our study, should display correlation coefficients in the 0.3 to 0.6 range, and our data support this.

However, even within the relatively narrow zone of the treeline ecotone, some differences in growth–temperature responses were due to site elevation. Specifically, at treeline sites, the responses to preceding autumn temperatures were consistently stronger, although this effect was often not statistically significant. Treeline trees are especially stressed due to loss of carbon from snow/ice abrasion and winter desiccation (Tranquillini 1979). In order to cope with winter losses, they require the longest possible growing season for maturation of needles, shoots, and buds and sufficient carbon storage (Oberhuber 2004). Compared to timberline stands, the growth response of treeline trees to mean monthly temperatures for the spring and for the peak growing season was delayed as a consequence of the later onset of the growing season.

We expected that treeline trees would display overall higher temperature sensitivity than timberline trees since they grow in a colder environment (Körner 1998). Chronologies derived from treeline trees reflected higher mean sensitivity, and treeline trees also had significantly thinner annual increments, along with a higher proportion of missing rings. All of these characteristics result from extreme climatic stress, but as shown by the lower correlation coefficients, the relationship of treeline chronologies to temperature means was weaker than that between timberline chronologies and monthly temperatures. This could be ascribed to treeline sites having a high proportion of young trees, as these are very sensitive to competition and environmental stressors (e.g. wind, snow redistribution, temperature extremes), which are largely not reflected in temperature means. Typically, growth–temperature relationships of juvenile trees are weaker even after removing the age effect (Carrer & Urbinati 2004). Additionally, treeline trees are more exposed to strong winds and rime, resulting in frequent damage to apical meristems, in which the hormones regulating radial growth are produced (Pallardy & Kozlowski 2008). As a consequence, non-temperature-driven TRW reductions occur. Similarly, in some other studies (Vittoz et al. 2008, Gruber et al. 2009), correlations were less significant for treeline than for timberline trees, and a less significant growth–temperature response has also been reported for wind-exposed stands (Oberhuber 2004). The majority of studies, including our own, thus show that in most cases, there is no gradient of increasing growth–temperature sensitivity with increasing elevation along the alpine treeline ecotone.

Aspect-related variations in growth–temperature responses were not homogenous across the 2 regions. Although in the Giant Mts. the north-facing timberline sites exhibited higher positive correlations with May temperatures when compared to south-facing sites, in the Hrubý Jeseník Mts. the south-facing timberline sites had higher positive correlations with April temperatures compared to north-facing slopes. This was probably related to regional differences in temperature and snow coverage. In the Hrubý Jeseník Mts., spring temperatures at timberline elevations are milder and snow pack depth is generally less (Květoň 2001, Migala 2005). This facilitates an overall earlier onset of the growing season on south-facing slopes in the Hrubý Jeseník Mts. However, in May, when the growing season generally begins at most locations throughout the Giant Mts. and Hrubý Jeseník Mts., the onset of radial growth depends on snow thawing, especially, in the case of the Giant Mts., on north-facing timberline sites. Based on our results as well as data from other mountain regions (Villalba et al. 1994, Kirchhefer 2001, Oberhuber 2004, Leonelli et al. 2009), aspect-induced variations in growth–temperature relationships are probably of greater ecological importance in those regions that are characterized by large altitudinal gradients, at high latitudes or in more continental areas than in the relatively wet and windy Sudetes Mts.

Interpreting relations between temperature means and growth rates also requires taking precipitation totals into account, because precipitation significantly affects growth of treeline trees in some mountain areas (e.g. Oberhuber et al. 2008, Saulnier et al. 2011). Therefore, we also analyzed the dependence of TRW on precipitation sums (not shown), but found only the precipitation sum of the previous growing season and March to have a consistent (but not statistically significant) effect at most sites (correlation coefficients ranging from 0.18 to 0.27). However, the effect of previous growing season precipitation might to some extent be a statistical artifact, since high summer precipitation implies low temperatures, and TRW indices are negatively correlated with preceding growing season temperatures (see Fig. 6). Moreover, the most extreme droughts (in 1947, 1976, and 2003, listed in Brázdil et al. 2009) in the Czech Republic were not reflected in our chronologies at all, with the most pronounced growth reductions related exclusively to negative temperature anomalies (in 1923, 1942, and 1974). Hence, we assume that treeline ecotone stands reflect a temperature signal alone, unlike stands in lower-elevation, montane forests of the Sudetes Mts. and nearby mountain chains that show mixed effects of precipitation and temperature (Sander et al. 1995, Kroupová 2001).

4.2. Treeline trends

At least in some regions, climatic signals captured in TRW variations across alpine treeline ecotones are thought to have changed during the last century (Wilson & Elling 2004, Büntgen et al. 2006, Carrer & Urbinati 2006, D'Arrigo et al. 2008). In our study in the Sudetes Mts., we identified distinct trends of decreasing growth sensitivity to preceding October temperatures and increasing sensitivity to May temperatures. The first trend probably resulted from an increase in growing season temperatures providing sufficient accumulation of carbon storage prior to October. The second has also been reported from the southern Italian Alpine arc (Carrer & Urbinati 2006) and has been related to an overall extension of the growing season in Europe (Menzel & Fabian 1999), in line with growing season changes observed in the Sudetes Mts. (Dubicka & Glowicki 2000). Sensitivity to peak growing season temperatures (June–July) has remained relatively stable in the Sudetes over the last century. However, we found that in the second half of the 20th century, the sensitivity increased in the Hrubý Jeseník Mts., probably due to the increasing proportion of older trees in the sampled stands. We did not find this in the chronologies from the Giant Mts., possibly because of pollution stress (Kroupová 2002). The drop in sensitivity to June–July and to preceding October temperatures recorded in the 1950s and 1960s is probably attributable to high proportions of juvenile trees at treeline sites, which probably had weaker reactions to temperatures.

Although we did not specifically focus on the age distribution of sampled trees, it is evident that most of the dominant trees emerged during the 20th century. This tendency was even more pronounced at treeline sites, in line with independent reports from other parts of the Hrubý Jeseník Mts. (Šenfeldr & Maděra 2011). Most treeline stands were established during the 1940s to 1960s, with the first culmination of radial increments dating to this period. The highest ring widths were achieved both at timberline and treeline sites at the end of the 1990s and from 2001 to 2010. This observation coincides with evidence from many mountain sites across central Europe (Rolland et al. 1998, Paulsen et al. 2000, Büntgen et al. 2007, 2008, 2010, Vittoz et al. 2008). Current growth rates of treeline sites in the Sudetes Mts. equal those of timberline sites during the 1960s and 1970s, which may illustrate pressure for an upward shift of the treeline ecotone. Throughout the whole study region, growth depressions in the 1970s and 1980s were followed by a period of intense growth recovery. All age classes of trees reached their highest ring width values during the last decade. This pattern, together with the predominance of juvenile specimens in treeline stands and trends in growth–temperature seasonality, indicates a strong upward shift of the treeline ecotone.

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A new tree-ring-based summer temperature reconstruction over the last three centuries for east-central Europe

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ABSTRACT: Tree rings and documentary evidence are the most important palaeoclimatic archives with annual resolution that continuously span several centuries. Despite this benefit, local to regional-scale temperature reconstructions and their spatial signatures tend to be irregularly distributed, and the appropriate extent of low-frequency variability captured in these proxy records remains uncertain. Here, the first summer temperature reconstruction from the Czech Sudetes Mountains that extends to 1700 AD was introduced. An ensemble reconstruction approach using 251 new high-elevation spruce ring width samples suggests particularly cold June–July temperatures at the beginning of the 18th century, in the 1740s and around 1820. Markedly warm conditions occurred in the 1790s and during the most recent decades. The reconstructed decadal summer temperature amplitude from 'Little Ice Age Cooling' to 'Recent Anthropogenic Warming' ranges from −3.5 °C between 1700 and 1710 to 1.3 °C in 1999–2009, with respect to the 1961–1990 mean climatology. Comparison of our new reconstruction with existing tree-ring chronologies from the Alps reveals a significant level of coherency that is much higher than the agreement with geographically closer documentary evidence from Central Europe. Our study confirms the importance of independent regional climate reconstructions, which capture the full range of past variability and also fill spatial gaps in large-scale networks.

KEY WORDS tree rings; climate reconstruction; dendroclimatology; documentary evidence; Little Ice Age; warming; Norway spruce; proxy archives; Sudetes

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1. Introduction

Evaluation of the long-term effects of climate change on ecosystems and societies requires the availability of high-resolution climate proxy archives that ideally extend, with annual resolution, beyond the period of instrumental measurements (Stenseth *et al.*, 2002; Büntgen *et al.*, 2011). The number of these pre-instrumental temperature reconstructions is growing (Jones *et al.*, 2009), and we are gradually obtaining a more consistent picture of the temperature range experienced between the coldest periods related to the so-called' Little Ice Age' and the most recent warming trend (Matthews and Briffa, 2005; Büntgen and Hellmann, 2014). Across Europe, these records have been inferred primarily from tree-ring and documentary records (Brázdil *et al.*, 2010; Büntgen *et al.*, 2010a). For example, there are numerous temperature-sensitive tree-ring chronologies from the Alps (e.g. Büntgen *et al.*, 2006), Pyrenees (Dorado-Liñán *et al.*, 2012), Carpathians (Popa and Kern, 2009; Büntgen *et al.*, 2013; Popa and Bouriaud, 2014) and Fennoscandia (Gunnarson *et al.*, 2011; Esper *et al.*, 2012). Temperature reconstructions from documentary evidence have also been established for several regions including Switzerland (Pfister, 1999), Germany (Glaser and Riemann, 2009), Poland (Przybylak *et al.*, 2005) and the Greater Alpine region (Casty *et al.*, 2005), while a monthly temperature reconstruction dating back to AD 1500 was recently compiled for Central Europe (CEU; Dobrovolný *et al.*, 2010).

However, there are still several research gaps associated with the spatial coverage of reconstructions (Büntgen *et al.*, 2010a), the coherence of reconstructions derived from different proxy sources (Jones *et al.*, 2009), and the preservation of low-frequency climate variability (Esper *et al.*, 2005a, 2005b). Additionally, the uncertainty attributed to standardization procedures is usually unknown as standardizing tree-ring proxies often require subjective decisions, and each procedure has its own assumptions, which might not be fully met with real tree-ring data sets (see, for example, Helama *et al.*, 2004; Briffa and Melvin, 2011; Hughes *et al.*, 2011). While the Regional Curve Standardization (RCS) method prominently retains low-frequency variability, individual curve-fitting techniques preserve a medium- to high-frequency signal, but in comparison with RCS, these techniques are less sensitive to variability in growth trends and the temporal distribution of tree-ring series (Melvin and Briffa, 2008).

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Both tree-ring chronologies and documentary data sets are irregularly distributed across Europe, and the number of temperature-sensitive tree-ring chronologies outside the highest alpine mountain ranges and high latitudes is very limited (Büntgen *et al.*, 2010a). The Sudetes (on the Czech-Polish border) are a region with scarce tree-ring data, spanning only the last two centuries (Sander *et al.*, 1995; Brázdil *et al.*, 1997; Treml *et al.*, 2012), and reliable instrumental temperature records from this region are missing for a large part of the 19th century (Migala, 2005).

As temperature-limited treeline ecotones are well developed in the Sudetes, the primary objective of this study was to build an extended tree-ring width (TRW) chronology for this region and to assess its climate sensitivity. Based on this chronology, we aimed to reconstruct summer temperatures prior to the period of instrumental station measurements (i.e. before 1881; Głowicki, 1998). Further, we assess the coherence, amplitude and spatial signature of significant cold and warm periods recorded in the new TRW-based reconstruction for the Sudetes, and compare our findings with existing TRW and documentary data sets from Central and Eastern Europe. Using an ensemble approach (Büntgen *et al.*, 2012), we placed special emphasis on the specification of uncertainty ranges associated with our TRW reconstruction, and therefore considered the effects of different standardization techniques and calibration trials.

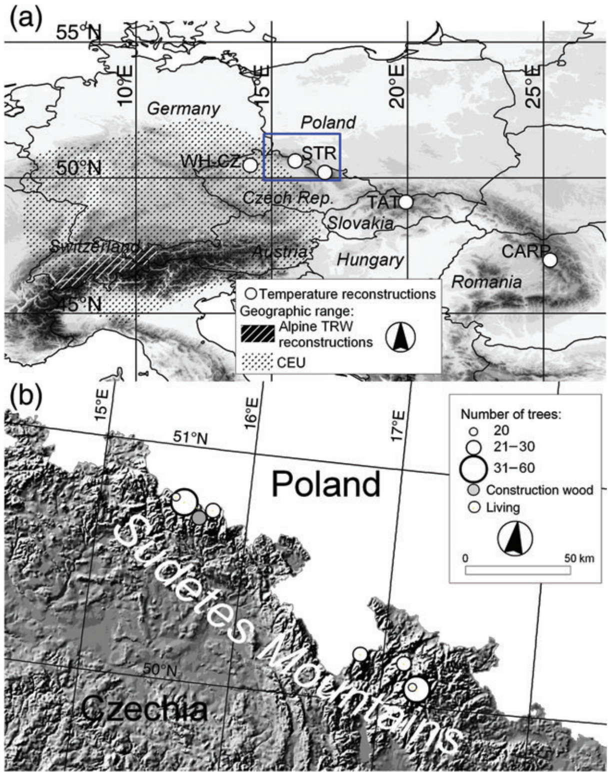

Figure 1. (a) Central and Eastern Europe with locations of individual temperature reconstructions. Alpine, TRW temperature reconstructions (ALP09, ALP11) are delineated as the region from which tree-ring series were used. The geographic range of the CEU temperature reconstruction is restricted to the area of the highest correlation with station data (Dobrovolný *et al.*, 2010). The rectangle denotes area captured on (b). (b) Study area with individual locations of tree-ring sites.

2. Data and methods

2.1. Geographical setting and tree-ring sampling

The Sudetes mountains in the Czech Republic comprise the Krkonoše Mts, Hrubý Jeseník Mts and Králický Sněžník Mts (Figure 1), with their summits reaching altitudes over 1400 m (Mt Sněžka, 1602 m). The mean annual air temperature at 1300 m asl fluctuates between 1.5 and 2.5 °C (1961–1990; Květoň, 2001; Migala, 2005), and the total annual precipitation ranges from 1200 mm in the eastern Sudetes to 1600 mm in the western Sudetes (Tolasz 2007). Mountain forests between 900 m asl and the treeline ecotone are primarily composed of Norway spruce (*Picea abies* [L.] Karst.), with the upper limit of closed forest (i.e. the lower boundary of the treeline ecotone) located around 1250–1400 m asl.

Increment cores from 280 living Norway spruce were collected at 13 locations in the Sudetes region (five in the Hrubý Jeseník and Králický Sněžník Mts, eight in the Krkonoše Mts). All sites were selected to represent relatively undisturbed old-growth stands between 1150 and 1350 m asl. Two cores per tree were taken to avoid eccentricity and compression wood owing to slope inclination and prevailing wind direction. In addition, 35 increment cores or cross-sections were collected from spruce construction timber from mountain huts situated above 1000 m in the Krkonoše Mts (Figure 1).

The cores were fixed on wooden supports and sanded. TRW was measured to the nearest 0.01 mm with a TimeTable measuring device (Vienna Institute for Archaeological Science). For each tree, mean TRW of both cores was used in subsequent analyses following visual cross-dating and missing ring identification using PAST4 software (Knibbe, 2004). Successfully cross-dated series of historical construction wood with values of mean sensitivity and mean TRW comparable with the living trees were included in the final data set and subsequently considered for standardization. The Sudetes master chronology was built after assessing the coherence of each of the 13 site chronologies.

Following the ensemble approach (Büntgen *et al.*, 2012), two versions of tree-ring series were considered: the data set 'all' includes all samples, while the data set 'pruned' contains pruned series, that is, tree-ring series were truncated at 150 years to avoid overrepresentation of old tree rings in the recent part of the chronology (Figure 2(a)). The following parameters were alternatively used in the detrending trials: (1) detrending function – spline with 50% variability cut-off at 200 years, spline with 50% variability cut-off at 66% of series length, negative exponential function and regional curve standardization; (2) index calculation: ratios or residuals after power transformation; and (3) variance stabilization: yes/no (Holmes *et al.*, 1986; Cook and Peters, 1997; Esper *et al.*, 2005a). Chronologies were processed using a signal-free approach

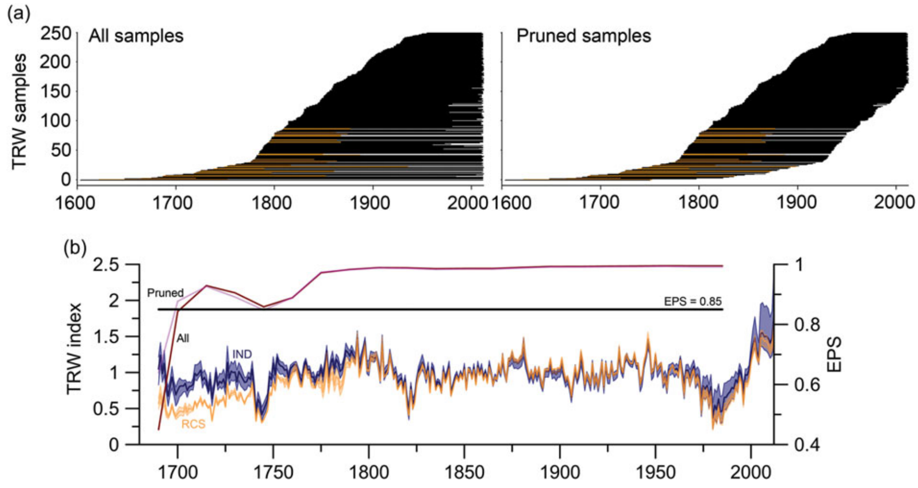

Figure 2. (a) Two basic data sets subjected to the detrending procedure – 'all' samples and 'pruned' samples. Wood from living trees is indicated by a black colour, the remaining samples come from historical wood; (b) Indexed TRW chronologies categorized by the detrending approach together with the EPS of detrended chronologies.

implemented in CRUST software (Melvin and Briffa, 2008; Melvin and Briffa, 2014). RCS chronologies were derived from the pruned data set only to prevent bias from an overrepresentation of 'old' tree rings in the recent part of chronology (Briffa and Melvin, 2011). All resulting chronologies were preliminary checked with respect to possible trend distortion at the end of the chronology. After removal of distorted chronologies (particularly splines and negative exponential-detrended chronologies with indices calculated as ratios), we ultimately worked with 22 standardized chronologies.

2.2. Response analyses and climate reconstruction

Consistent with the ensemble approach described earlier, three temperature data sets were used as calibration targets for the proxy records. The temperature series differed mainly in their spatial coverage. Station data from Mt Sněžka in the Krkonoše Mts (1602 m; Głowicki, 1998, covering the period from 1881 to 2006) and the 2.5° and 0.5° gridded CRU 3.2 data sets were used, each covering the period from 1901 to 2009 (Mitchell and Jones, 2005, updated). The spatial signature of the temperature data set from Mt Sněžka was checked against station data from Mt Praděd situated in the eastern part of the Sudetes. The temperature time series from Mt Praděd covers the period from 1946 to 1990. Only monthly temperature means for each year from all data sets were considered. To assess the similarity between individual temperature time series, Pearson correlation coefficients were computed.

Next, all TRW chronologies with the three aforementioned temperature data sets were correlated during the common period (1902–2006). Monthly mean temperatures over the so-called 'dendrochronological year' (from May of the year preceding ring formation until September of the ring formation year) were used (Fritts, 1976). Various seasonal means were also considered. The best-correlated temperature variable was then selected for temperature reconstruction.

To test temporal stability of the climate–growth relationship, moving correlations between the best-correlated temperature variable and indexed TRW were computed for 31-year moving window periods. Correlations were also computed for low- and high-pass-filtered temperatures and TRW chronologies.

The best-correlated temperature variable was further checked for reconstruction skill through scaling and a regression transfer function (Esper *et al.*, 2005a). The reconstruction ability of chronologies was measured over late and early calibration/verification intervals using R^2, reduction of error (RE) and coefficient of efficiency (CE) statistics (Nash and Sutcliffe, 1971; Fritts *et al.*, 1992). Scaling of TRW indices was preferred over regression transfer to preserve the variance of temperatures in the final reconstruction (Esper *et al.*, 2005a). The longest possible period (1901–1970, for an explanation see the Results section) was selected to compute the means and standard deviations (SD) of TRW indices as well as the target temperature variable.

Because the potential for preserving low-frequency variability differed among the various detrending approaches (Helama *et al.*, 2004), two basic reconstructions were made: RCS and individual detrending-based (IND; spline and negative exponential detrending) reconstructions.

The uncertainty ranges of both temperature reconstructions were computed using the uncertainty range derived from detrending and the calibration error (Büntgen *et al.*, 2013). The final IND and RCS reconstructions were therefore represented by the reconstructed mean value of temperature buffered by the minimum and maximum values resulting from the various detrending trials. By adding the corresponding root-mean-square errors (±RMSE), the uncertainty buffers, herein computed over the calibration period, were further extended.

The spatial signature of the Sudetes chronology was computed using the gridded CRU TS 3.2 data set (Mitchell and Jones, 2005). The Sudetes temperature reconstruction was further compared with available reconstructions of summer temperatures covering Central and Eastern Europe. Both tree-ring and documentary data were included (Table 1). The comparison was based on correlation coefficients of original time series and time series filtered by low- and high-pass Gaussian filters (Büntgen *et al.*, 2010b). In addition, 31-year moving correlations between the Sudetes and other chronologies were computed. Principal component analysis with normalized varimax rotation was applied to examine the main statistically significant directions of variability among the reconstructions under comparison (Richman, 1986). For each reconstruction, we also computed the amplitude of temperature means averaged over 11- to 21-year windows.

Table 1. Overview of compared temperature reconstructions.

Reconstruction	Period	Elevation (m a.s.l.)	Longitude/ Latitude	Proxy	Reconstructed temperature variable	Region	Source
Tatra Mts (TAT)	AD 1040–2011	800–1500	19°E/52°N	TRW	June–July	The Tatra Mts (Slovakia)	Büntgen *et al.* (2013)
Carpathians (CAR09)	AD 1036–2005	1750–1800	25°15′E/47°15′N	TRW	June–July	The East Carpathians (Romania)	Popa and Kern (2009)
Alps (ALP09)	AD 500–2003	1450–2300	19°E/51°N	TRW	June–July	Alpine Region	Büntgen *et al.* (2011)
Alps (ALP11)	AD 951–2004	1450–2300	7°50′E/46°25′N	TRW	June–July	Alpine Region	Büntgen *et al.* (2009)
Czech Lands wheat harvest (WH-CZ)	AD 1501–2008	lowlands	14′E/50′N	Wheat harvest dates	March–June	Czech Lands (Czech Republic)	Možný *et al.* (2012)
Central Europe (CEU)	AD 1500–2007	Variant, mostly lowlands	47–50°N/6–18°E	Documentary and instrumental data	June–July	Central Europe (Austria, Czechia, Germany, Switzerland)	Dobrovolný *et al.* (2010)

3. Results

3.1. Regional growth trends and chronology characteristics

Tree-ring series from 251 trees in 13 locations distributed across the highest mountain ranges in the Sudetes reveal high inter-correlation, which enables the construction of a single regional chronology. Correlations between individual site chronologies range from 0.69 to 0.88 over the common period (since 1870). Twenty-two series of historical wood from the Krkonoše Mts were also included. The final regional chronology extends back to 1690 with more than ten series (Figure 2). Both juvenile and mature trees are represented within all sections of the chronology, although their age representation is more balanced in the 'pruned' data set (Figure 2(a)).

Mean TRW was 1.40 mm, with an obvious age trend and corresponding higher growth rate in short series and smaller average growth rate in long series. Mean sensitivity of the raw series was similar for the 'pruned' (0.208) and 'all' (0.214) data sets. The expressed population signal (EPS) is consistently above the 0.85 threshold back to 1700 (Figure 2(b)). Compared with chronologies built from the 'all' series, the chronologies constructed from 'pruned' series show higher values of EPS at the beginning of the chronology. RCS chronologies display slightly greater mean sensitivity compared with IND chronologies (Table 2). The difference between RCS and individual-based detrending chronologies is highest in the early part of the chronology, before ~1750. After the year 2000, the difference between RCS and IND chronologies results particularly from inflated TRW indices of IND chronologies with indices calculated as ratios (Figure 2(b)). Although low-frequency variability differs between RCS and IND chronologies, high-frequency variability is similar irrespective of the detrending approach.

Table 2. Basic characteristics of individual TRW data sets.

Data set	Chronology span	Chronology span ≥10 series	Number of series	Mean segment length	Mean TRW	EPS ≥ 0.85 (30 years moving window with 15 years overlap)	Mean sensitivity (average values ind. detrend./RCS)
All	1603–2012	1689	251	163	1.497	1700	0.159/0.164
Pruned	1603–2012	1689	251	131	1.611	1700	0.157/0.165

3.2. Growth-climate response patterns

Correlations between target temperature data on a monthly basis range from 0.68 to 0.99. The relatively low correlation coefficients between gridded and station data ($r = 0.68–0.90$) were characteristic features for the November to February monthly means. Correlations between monthly temperature means of station data (Mt Sněžka and Mt Praděd) were always high (≥0.98), indicating good spatial coverage of the Sněžka station data encompassing the entire Sudetes region. Considering the low-frequency domain, trends of CRU and Sněžka data slightly differ between the 1950s and 1970s, and at the beginning of the 20th century (Figure 3(b)).

Over the entire proxy–target overlap (1901–2006), the strongest correlations were found between TRW and monthly temperature means in June and July as well as in a June–July seasonal mean, irrespective of the source temperature data (Figure 4(a)). Correlations between TRW indices and June–July temperatures range from 0.46 (‘pruned’ power-transformed series detrended by RCS, indices calculated as residuals) to 0.62 (‘all’ series detrended using a spline with 50% variability cut-off at 66% series length, indices calculated as residuals). Overall, correlations of TRW with temperatures in the low-frequency domain are stronger than correlations in the high-frequency domain (Figure 4(b)). However, the 50-year low-pass-filtered data, particularly for the RCS chronologies, show relatively weaker agreement with temperatures measured at the Sněžka station, because of the lagged and deeper depression in TRW compared with measured temperatures in 1970s and 1980s (Figure 3).

The moving 31-year correlations between TRW and June–July temperature means show decreases in temperature sensitivity mainly after 1970 and to some extent before 1920 (Figure 4(c)). The strongest relationships found are with Sněžka station data, for which the moving correlations do not drop below 0.40 over the entire period 1901–2006 and are higher than 0.5 from 1901 to the end of the 1960s. Therefore, the period 1901–1970 for the Snezka station data was selected as a calibration–verification interval in our reconstruction.

3.3. Reconstructed temperature variability

Transfer functions based on both linear regression and scaling are efficient at reconstructing temperatures, as indicated by the calibration–verification statistics (Table 3).

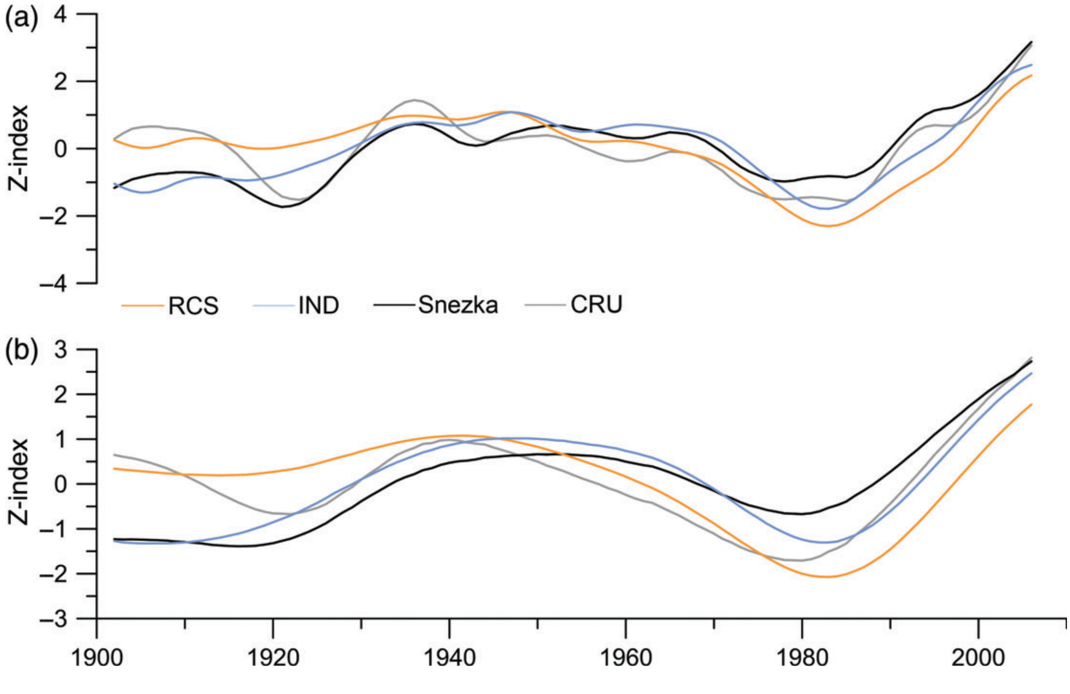

Figure 3. Z-Transformed low-passed temperature targets (Snezka station data, CRU 3.2 2.5° resolution) and tree-ring chronologies. (a) 20-year low-pass filter; (b) 50-year low-pass filter.

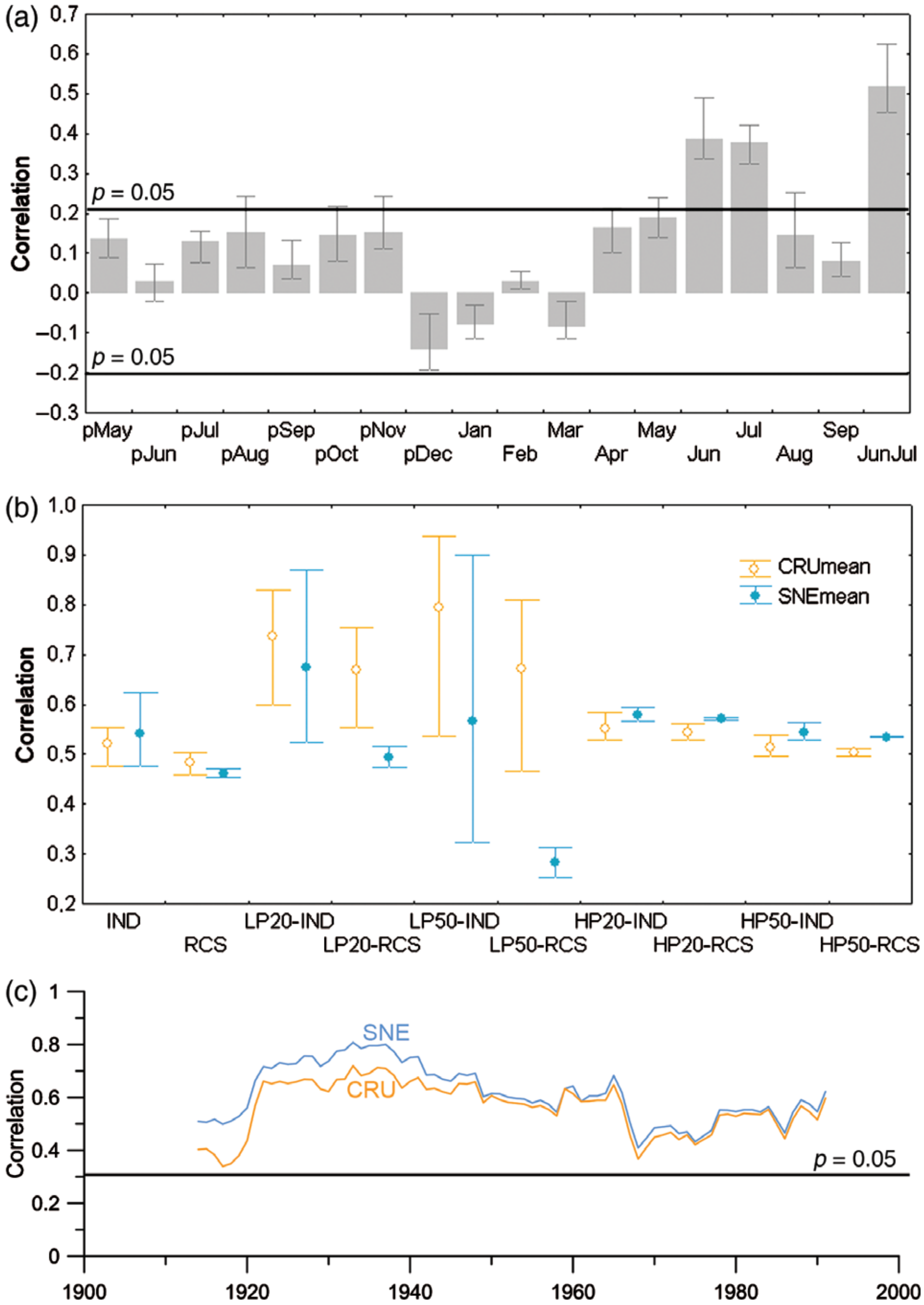

Figure 4. (a) Range (maximum, minimum and mean) of correlation coefficients between individual TRW chronologies and monthly temperature means of various temperature targets (CRU 2.5° grid – Sudetes; CRU 0.5° grid – JeseníkyMts; CRU 0.5° grid – KrkonošeMts; Sněžka station data) over the 1902–2006 period; (b) Correlations of TRW chronologies (unfiltered, smoothed by Gaussian low- and high-pass filters with window lengths of 20 and 50 years) with June–July temperatures categorized according to detrending approach; (c) 31-year moving correlations between June–July temperatures and TRW indices. Average values for all chronologies are presented.

The regression transfer function reveals slightly higher reconstruction skill according to CE and RE (Table 3); however, it tends to underestimate temperature variability and amplitudes (Figure 5). SD values of scaled temperatures and Sněžka station temperatures are comparable (0.98 and 1.00, respectively), and nearly twice as high as the SD of regressed temperatures (0.59). Thus, to preserve temperature amplitudes and variability, only a scaling approach was considered (Figure 4). Two temperature reconstructions were obtained – an RCS-based reconstruction (STR-RCS) and an individual detrending-based reconstruction (STR-IND) (Figure 6(a)). The uncertainty attributable to detrending approach ranges from 1.2 °C (STR-IND) to 0.90 °C (STR-RCS). Uncertainty buffer is further extended by RMSE 0.67 °C, which is the average value for all calibration–verification trials. As expected, the RCS-based reconstruction reveals more low-frequency variability than the individual-based detrending temperature reconstruction. Reconstructions show two pronounced periods of increased temperatures: at the turn of the 18th and 19th centuries (1787–1797 + 1.9 °C anomaly by STR-IND) and

Table 3. Results of verification statistics.

	Early calibration period (1901–1935)			Late calibration period (1936–1970)		
	R^2	RE	CE	R^2	RE	CE
Regression	0.42	0.56	0.37	0.33	0.46	0.27
Scaling	0.42	0.52	0.33	0.33	0.38	0.20

between 1870 and 1880 (1873–1883 + 1.3 °C anomaly by STR-RCS; Figure 6(a)). Both tree rings and instrumental data confirmed that the 1950s and the last 10 years (after 2000) belonged to warmest periods. The warmest years according to the reconstruction were 1794 (+3.0 °C anomaly identified by STR-RCS and +3.4 °C anomaly by STR-IND), 1798, 1881, 1946, 2002 and 2006 (+3.8 °C; the last three are based on instrumental data). Periods of low temperatures occurred mainly in the early part of the reconstructed time series leading up to 1730 (1700–1710, −3.5 °C anomaly by STR-RCS), between 1737 and 1747 (−2.3 °C anomaly by STR-IND), between 1816 and 1826 (−1.7; −2.1 °C anomaly by STR-IND and STR-RCS, respectively) and, based on instrumental data, in the 1970s and 1980s. The lowest reconstructed June–July temperatures occur in 1744 (−4.7 °C anomaly identified by STR-RCS and −4.1 °C by STR-IND) and in 1821 (−4.0 °C by both STR-RCS and STR-IND).

The spatial signature of the Sudetes chronology mainly encompasses the areas of the Czech Republic, Slovakia, south Poland, east Austria and Hungary (Figure 6(b)). In the late part of the study period (1956–2009), the area with the highest correlations shifts eastward.

3.4. Comparison with other temperature reconstructions

The Alpine ALP11 chronology is most similar to the Sudetes reconstructions (both to STR-IND and to STR-RCS) in terms of its correlation coefficient (Figure 7). In general, reconstructions from the Czech Lands wheat harvest (WH-CZ, CEU) and both Alpine reconstructions agree more with the Sudetes temperature reconstruction (STR) than with Carpathian reconstructions. The similarity between the Sudetes and Alpine ALP11 or between Czech wheat harvest reconstructions is larger in the low-frequency domain. Carpathian and CEU reconstructions, by contrast, are closer to those of the Sudetes in the high-frequency domain (Figure 6). The most stable moving correlations found were with the ALP11 time series; these correlations were mostly statistically significant (Figure 8(b)). From 1760 onwards, the correlations with the CEU reconstruction are also relatively stable and significant. The moving correlations with other temperature reconstructions are rather weak or unstable.

Our principal component analysis (Figure 8(c)) shows that Carpathian and Alpine reconstructions load two distinct patterns in each of the examined centuries. The remaining reconstructions (STR, CEU and WH-CZ) are more similar in recent years (20th century) than in the 18th and 19th centuries, when they formed separate components (Figure 8(c)).

Common negative anomalies occur in the 1740s and around 1820, for both Sudetes reconstructions and for the remaining TRW-based reconstructions (Figure 8(a)). However, the distinct positive anomaly at the end of the 18th century recorded in the Sudetes reconstruction is displayed only in the WH-CZ reconstruction.

The most distinct negative temperature anomalies that occurred over 11-year periods were approximately 1.6–3.5 °C (mean value: −2.6 °C) lower compared with the reference mean temperature (1961–1990) for TRW-based reconstructions (Table 4). Documentary or instrument-based reconstructions revealed smaller anomalies approaching −1 °C. The coldest periods recorded in the STR are concentrated in the early 18th century and in the 1740s, whereas other reconstructions display their coldest 11 years around 1815. Period of 21 years revealed

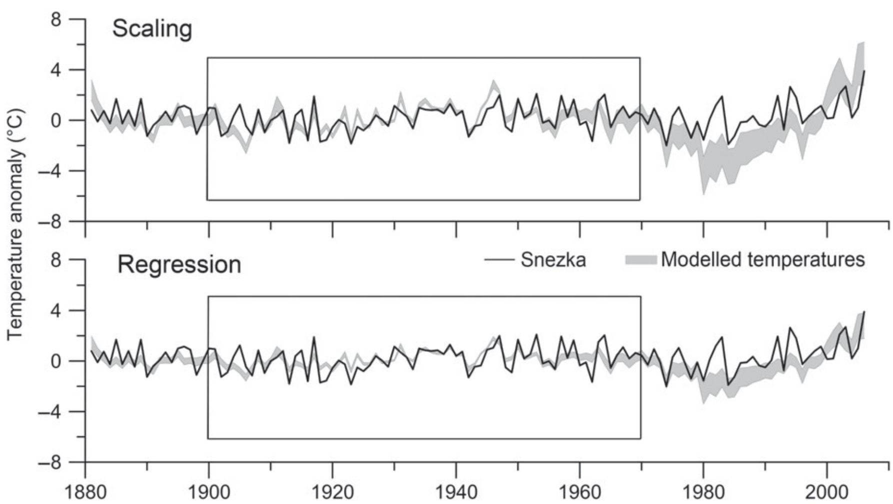

Figure 5. June–July temperatures modelled by scaling and regression. Modelled temperatures are expressed as the range between their highest and lowest values in a given year depending on detrending approach. Measured temperatures from Sněžka station are presented as well. The rectangle denotes the interval of the proxy–target overlap used for scaling and for the regression transfer function.

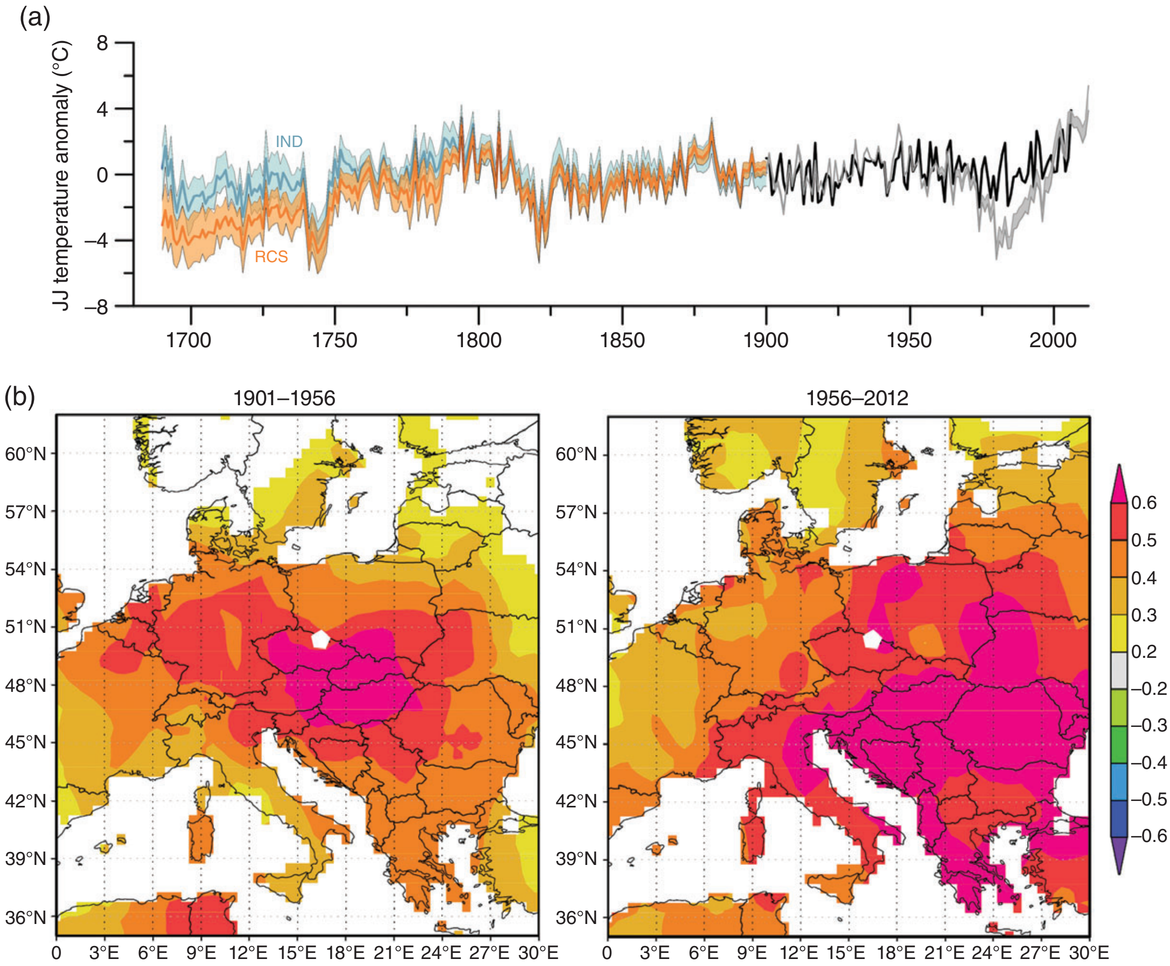

Figure 6. (a) Reconstructed June–July temperatures based on tree-ring chronologies from the Sudetes. Temperatures are expressed as departures from the temperature mean of the reference period 1961–1990. Lines denote the mean values; buffers include uncertainty attributed to detrending approach and RMSE. From 1900 onwards, only instrumental temperatures from Snezka station (black) and scaled TRW indices (grey) are presented. (b) Spatial signature of correlations between the mean Sudetes TRW chronology and June–July temperatures. Position of the area from which the chronology was derived is indicated by a white pentagon. Correlations were computed using KNMI Climate Explorer website (Trouet and van Oldenborgh, 2013).

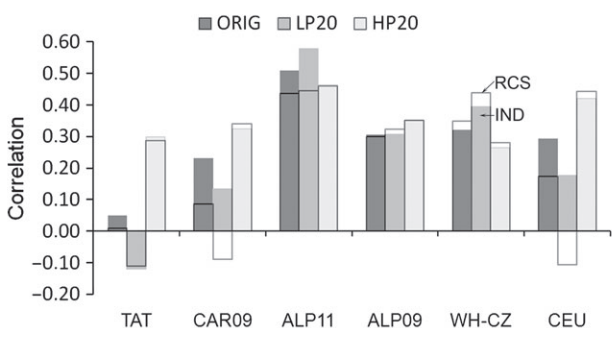

Figure 7. Correlations between Sudetes temperature reconstruction and other temperature reconstructions over the period of overlap (1700–1970). ORIG: original data; LP20: 20-year low-pass filter; HP20: 20-year high-pass filter. STR-IND is represented by filled columns, STR-RCS by blank columns.

a similar temporal pattern; however, the anomalies are, of course, smaller (Table 4).

4. Discussion

The STR covers a period reaching back to 1700, which is significantly longer than the period for which dendrochronological and instrumental data are available from this region (Sander *et al.*, 1995: period 1781–1991; Brázdil *et al.*, 1997: 1804–1989; Głowicki, 1998: 1881–2006). The STR indicates the cold period at the beginning of the 18th century and cold spells in the 1740s, and around 1820 were characterized by temperatures approximately 2 °C lower (individual-based detrending) or more than 3 °C lower (RCS detrending) on the decadal scale compared with the reference period of 1961–1990. Carbon-stable isotopes from oak tree rings indicate that the exact same periods were the coldest of the last three centuries in south-west Poland (Jedrysek *et al.*, 2003). The cold spell between 1816 and 1826 is related to the Tambora volcanic eruption (Oppenheimer 2003) and to the Dalton minimum of solar activity (Reimer *et al.*, 2004), which has been similarly recorded in a reconstruction based on late-wood density from the Krkonoše Mountains

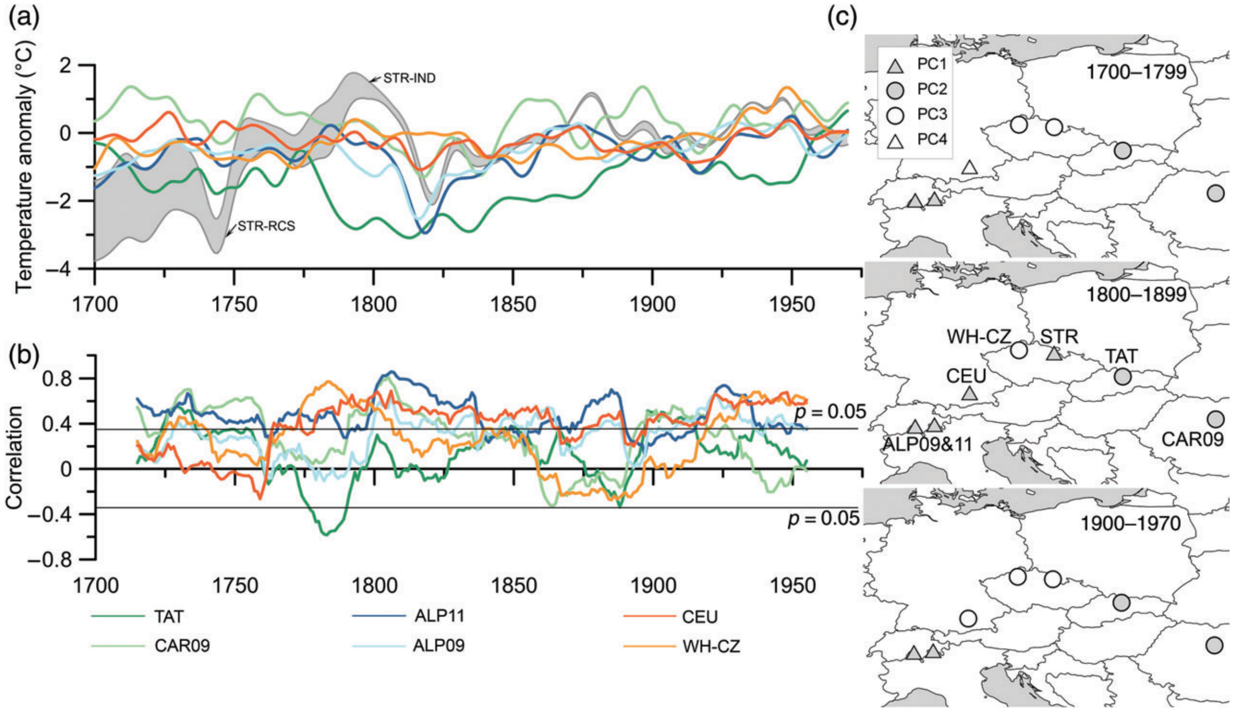

Figure 8. (a) Temperature reconstructions of June–July temperatures together with the new Sudetes TRW-based reconstruction. As an exception, the wheat harvest reconstruction is valid for March–June temperatures. The time series are smoothed with a 20-year low-pass Gaussian filter. (b) Moving correlations between the Sudetes June–July reconstruction and other temperature time series. The correlations are computed for 31-year windows. (c) Significant principal components indicating spatial variability of temperature reconstructions in the 18th, 19th and 20th centuries. Note that for B and C, differences between STR-IND and STR-RCS were negligible. For the sake of simplicity, only STR-IND is presented.

(Brázdil *et al.*, 1997). The late-wood density reconstruction displays a smaller and shorter negative anomaly, likely associated with the regression transfer function used in that study and with the relatively low autocorrelation within the late-wood density data compared with TRW chronologies (Sander *et al.*, 1995).

Other than recent warming in the 1990s and 2000s, the most pronounced positive temperature anomaly was recorded at the end of the 18th century, when 11-year average temperatures were higher by 1.3 °C (STR-RCS) or 1.8 °C (STR-IND) compared with the reference period. The same warm period was recorded in the adjacent part of Poland (Jedrysek *et al.*, 2003) and in the Alps (Casty *et al.*, 2005). Enhanced tree growth was thus largely associated with increased summer temperatures, at least in CEU. However, at the end of the 18th century, several heavy windstorms were also recorded in the Sudetes (Nožička 1957), and in the same period, a distinct increase in tree establishment is recorded in our data (Figure 2(a)). Therefore, the growth release evident in the tree rings at the end of the 18th century might also be associated to some extent with open canopies after windthrows. Contemporary spruce growth rates (i.e. since the 1990s) are similar (STR-RCS) or exceed (STR-IND) those from the end of the 18th century, corresponding to findings reported for fir and larch in Central and Eastern Europe (Büntgen *et al.*, 2013, 2014).

Both of the Sudetes temperature reconstruction (STR-IND and STR-RCS) show high temperature amplitudes. The end of the Maunder minimum of solar activity period (AD: 1645–1715, Reimer *et al.*, 2004) was colder by 4.5 °C compared with the 1790s and up to 4.8 °C colder compared with the 2000s, considering both the decadal temperature means and the RCS reconstruction. Differences between the coldest and the warmest years in the last three centuries exceeded 8 °C for both STR-RCS and IND. Documentary-based reconstructions from adjacent regions reported amplitudes of annual extremes approximately 1 °C lower (CEU; Dobrovolný *et al.*, 2010) or as much as 2 °C lower (WH-CZ; Možný *et al.*, 2012) than STR. Reconstructed decadal-scale amplitudes differed between STR and documentary-based reconstructions by 2 (WH-CZ) to 2.5 °C (CEU).

Table 4. Greatest negative temperature anomalies from the reference period of 1961–1990.

Reconstruction	11-year period	11-year value (temperature anomaly), °C	21-year period	21-year value (temperature anomaly), °C
TAT	1806–1816	−3.1	1802–1822	−2.9
CAR09	1813–1823	−1.6	1806–1826	−0.9
ALP11	1813–1823	−2.9	1813–1833	−2.2
ALP09	1811–1821	−2.6	1812–1832	−1.9
WH-CZ	1766–1776	−1.1	1756–1776	−0.9
CEU	1813–1823	−1.2	1906–1926	−0.9
STR-IND	1737–1747	−2.3	1729–1759	−1.4
STR-RCS	1700–1710	−3.5	1700–1720	−3.3

As our reconstruction focused on the preservation of low-frequency variability (Esper *et al.*, 2005a), we consider the newly reconstructed amplitudes as realistic. Moreover, the applied ensemble approach enables estimation of uncertainty attributed to the standardization procedure and calibration error. For STR, both of these components of uncertainty have approximately the same value, ranging between 0.6 and 1.2 °C with uncertainty attributed to calibration being slightly less than that of standardization procedure.

In this study, the different affinities of low-pass filtered RCS chronologies to Sněžka and CRU temperature data were also observed. It might be attributed to possible homogeneity bias in the Sněžka station temperature series owing to the change in the position of the thermometer between 1899 and 1900 (Głowicki, 1998). In addition to a possible homogeneity bias, the mesoclimatic conditions of the station at the 1602 m isolated summit of Mt Sněžka might influence its temperature trend (Weber *et al.*, 1997). Furthermore, low-passed RCS chronologies were especially sensitive to weakening of climate–growth relations associated with acid deposition in 1970s and 1980s (Sander *et al.*, 1995; Treml *et al.*, 2012).

In terms of its spatial signature, the STR correlates well with June–July gridded temperatures across the vast region of eastern-central Europe throughout the 20th century. At the same time, the correlations of the STR over the full record (three centuries) are higher with Alpine than with eastern-European (Carpathian) TRW reconstructions. This might indicate a shift in the spatial pattern of summer temperatures in CEU and a stronger association with Eastern Europe in the 20th century than in the 18th and 19th centuries. Species-specific climate–growth responses (Büntgen *et al.*, 2007; Babst *et al.*, 2013) might also play a role, however, because Carpathian chronologies are derived from Swiss stone pine and larch whereas spruce prevails in reconstructions for the Alps and Sudetes. Nevertheless, Frank and Esper (2005) argue that the effect of tree species on climate reconstructions is negligible, citing the examples of Norway spruce, European larch and Swiss stone pine – the species from which the compared chronologies in our study were derived.

The dominant negative anomalies (in the 1740s and after 1816) are common to all TRW temperature reconstructions under comparison, but they differ in length and magnitude. Compared with Alpine chronologies, the STR cold and warm spells in the 1740s and at the end of the 18th century, respectively, are more pronounced, and the cold spell after 1816 is longer. This appears to be a general trend in the northward direction from the Alpine arc, as also shown by Wilson *et al.* (2005). According to their study, TRW chronologies from medium-altitude mountain ranges in CEU (Harz, Bavarian Forest, Krkonoše Mts) represent a separate group differing both from Alpine chronologies and from chronologies for the Western Carpathians. Wilson *et al.* (2005) report a boundary in TRW patterns between the southern and northern parts of the Czech Republic. The spatial signature of the STR reveals a similar location of the divide along the south-western boundary of the Czech Republic. Although evaluated reconstructions across CEU show heterogeneity, the primary negative and positive temperature anomalies recorded in the STR (i.e. the cold spells at the beginning of the 18th century, in the 1740s, and around 1820 and the warm period in the 1790s) correspond well with available reconstructions from more distant areas [e.g. with Greater Alpine region (Casty *et al.*, 2005) and even with a robust reconstruction of the entire Northern Hemisphere (Briffa *et al.*, 2001)]. This suggests a general agreement between low-frequency temperature variations in the north-eastern part of Central Europe and those in both the Alpine region and in Northern Europe.

By comparing TRW- and documentary-based temperature reconstructions, the temporal stability of the reconstructions can be assessed. For example, moving correlations between the STR and the CEU temperature reconstructions are low until the 1760s, when they increased abruptly. Since the 1760s, the CEU reconstruction is based on the longest temperature record; therefore, its uncertainty range is lower (Dobrovolný *et al.*, 2010), resulting in the abrupt increase in correlations with the STR.

Surprisingly, the Sudetes temperature reconstruction is more similar in terms of its correlation coefficients to Alpine TRW-based reconstructions than to geographically closer temperature reconstructions from the Czech Lands (WH-CZ; Možný *et al.*, 2012) or from the broader area of Central Europe (Dobrovolný *et al.*, 2010). There are at least three possible explanations: (1) TRW chronologies might be more similar to each other than to reconstructions based on other types of data owing to the biophysical properties of tree-ring formation. In addition to temperatures in the peak growing season, radial increments of trees in cold environments often reflect the temperature signals of the early growing season or even the preceding autumn (Oberhuber, 2004; Büntgen *et al.*, 2007; Treml *et al.*, 2012). (2) TRW-based reconstructions probably preserve more low-frequency variability than indexed documentary data, which is consistent with the substantial agreement between the STR and wheat harvest temperature reconstructions (Možný *et al.*, 2012) and with the near absence of correlation between STR and CEU reconstructions in the low-frequency domain. Documentary reconstructions based on biophysical or physical institutional records, such as WH-CZ, probably preserve a relatively larger portion of low-frequency variation than reconstructions based on indexed weather descriptions (Zorita *et al.*, 2010). (3) Because we compared lowland documentary data with TRW data from high elevations, differences in temperature trends and amplitudes of temperature oscillations between high elevations and lowlands also have to be taken into account (Weber *et al.*, 1997; Ceppi *et al.*, 2012). Our comparison of tree-ring with documentary-based reconstructions illustrated a more general phenomenon – while tree-ring-based temperature reconstructions originate from remote regions at high latitudes and high elevations (Büntgen *et al.*, 2010a), documentary-based temperature reconstructions and the longest instrumental records usually come from densely populated lowland areas (Brázdil *et al.*, 2010).

5. Conclusions

Our new summer temperature reconstruction from the Czech Sudetes Mountains, spatially representing most of east-central Europe and extending back to 1700, indicates that the coldest June–July period at the beginning of the 18th century was approximately −3.5 to −2.3 °C cooler than the reference period 1961–1990. The warmest periods in the 1790s and from 2000–2009 were 1.3–1.9 °C warmer than the reference mean. This temperature range results from different standardization and calibration procedures. In comparison with available documentary-based reconstructions, our reconstructed decadal-scale temperature amplitudes were approximately 2–2.5 °C greater. We demonstrated higher coherency between distant high-elevation tree-ring reconstructions compared with geographically closer reconstructions based on lowland documentary data. The reasons behind this are likely associated with better ability of tree rings to preserve low-frequency signal, but altitudinal divergences of proxy source areas and intrinsic properties of documentary and tree-ring data cannot be disregarded. Observed differences between tree-ring and documentary-based reconstructions further emphasized the need for the new regional reconstructions based on different proxies and capturing the full range of past climatic variability. Moreover, the reliability of TRW-based reconstructions can be further increased by definition of possible uncertainty ranges. The ensemble approach applied in our study showed that uncertainty buffers attributed to standardization are similar to those of calibration being between 0.6 and 1.2 °C.

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Trees
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ORIGINAL ARTICLE

Growth trends and climate responses of Norway spruce along elevational gradients in East-Central Europe

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Abstract

Key message **Decadal growth variability of Norway spruce increases with elevation. Recent temperature sensitivity and growth enhancement are limited to trees growing in the zone adjacent to timberline.**

Abstract Growth trends and climate responses of forest trees along elevational gradients are not fully understood. A deeper insight is, however, fundamental for predicting ecosystem functioning and productivity under future climate change. Supplementary to the effects of elevation and regional provenance on tree growth are sample depth, uneven representation of sample age and varying site conditions. Furthermore, there is only a limited number of studies addressing growth changes along elevational gradients, while at the same time applying tree-ring standardization methods that are sensitive to trend preservation. Here, we introduce 12 novel tree-ring width chronologies of Norway spruce (*Picea abies*[L.] Karst.) from four elevational belts encompassing montane forests and the local timberline in three regions in East-Central Europe between 15° and 19°E. Each chronology is characterized by sufficient sample replication and a comparable age structure between 1906 and 2010. Tree growth near timberline revealed substantial medium-frequency variability and sharply increasing ring widths since the 1980s. Medium-frequency growth variability of lower elevation trees was, however, relatively small, and growth rates over the last decade were either stable or even decreased. During the last four decades, Norway spruce from higher elevations exhibited a reduced response to autumn temperatures preceding ring formation. In contrast, trees from the lower-montane zone increased their sensitivity to drought during the same time. Our results emphasize not only different but also instable growth trends and climate responses of forest trees along altitudinal gradients, which should be considered in future forest management strategies.

Keywords Climate change · Mountain forests · *Picea abies* · Radial growth · Tree rings · Trend preservation

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Introduction

Tree growth responses to ongoing climate change are of special importance because forest ecosystems are one of the most productive components of the Earth's biosphere (Pan et al. 2011). Cell walls of woody tissues represent a considerable sink of atmospheric carbon, with changes in wood formation playing an important role in the carbon cycle (Luyssaert et al. 2008). Global warming can cause forest ecosystems to either decrease in productivity from increased drought or increase in productivity from rising temperatures (Babst et al. 2013; Schuster and Oberhuber 2013). Negative and positive effects on forest productivity

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may even vary at local or regional scales, with particularly distinct differences occurring along altitudinal gradients (Mäkinen et al. 2002; King et al. 2013). Reconstructing the dynamics of forest productivity at decadal to centennial time-scales requires precise estimates of past growth trends (Melvin and Briffa 2008; Biondi and Qeadan 2008; Büntgen et al. 2012; Babst et al. 2014). However, appropriate methodologies that capture the full range of high to low frequency growth variability along environmental gradients are still limited.

Dynamics in forest tree growth are best reconstructed via radial increments (Graumlich et al. 1989; Nehrbass-Ahles et al. 2014). In woody plants, growth rings are closely related to environmental conditions (Schweingruber 1996), and their sensitivity often follows seasonal patterns of water availability and/or temperature (Fritts 1976). For species with broad elevational ranges, mountain regions with their pronounced elevational gradients present the opportunity to investigate climatic drivers of radial growth under both, relatively cool and warm conditions (Körner 2007). Studies along elevational gradients therefore appear particularly helpful in discovering species-specific growth sensitivity to ambient climate variability.

In central and eastern Europe, Norway spruce, (*Picea abies* [L.] Karst.) is one of the economically most important forest species native to mountain habitats (Spiecker et al. 1996), spanning a natural range from the montane zone up to treeline. Several studies have investigated elevation-dependent growth–climate responses of Norway spruce, e.g. in southwestern and eastern Germany (Mäkinen et al. 2002, 2003; Dittmar et al. 2012), the northern Alps (Leal et al. 2007; Hartl-Meier et al. 2014a, b), the Bavarian Forest (Wilson and Hopfmueller 2001; Čejková and Kolář 2009), the northern part of the Babia Góra Mountains (Bednarz et al. 1999; Kaczka et al. 2015), the Tatra Mountains (Savva et al. 2006; Büntgen et al. 2007), and the eastern Carpathians (Kaczka and Büntgen 2006; Sidor et al. 2015). These studies generally report temperature-controlled radial growth at higher elevations, mixed effects of precipitation and temperature at middle elevations (around 700–1000 m a.s.l), and overall drought-limited ring widths at lower elevations (Mäkinen et al. 2003; Babst et al. 2013). Focussing on growth–climate responses alone, the majority of the above-mentioned studies, however, did not specifically consider elevational-dependent changes in growth trends and rates.

The comparability of datasets used in previous studies of changing growth patterns along elevational gradients is often limited, thus hampering the analysis of subtle changes in growth trends. Common issues include considerable differences in the distribution of study sites along elevational gradients and their relative position towards timberline, varying sample depths and tree-ring series lengths, as well as different age structures (i.e. varying proportion between juvenile and adult rings). As a result, differences in growth trends and variations between elevational zones might be over- or underestimated (Briffa and Melvin 2011; Bowman et al. 2013; Babst et al. 2014; Düthorn et al. 2015). Nevertheless, decadal-scale growth variability is of great interest because it approximately allows tracking the pace of ongoing and predicted climate change. Traditional dendrochronological approaches based on direct curve-fitting to the raw tree-ring series might lead to so-called trend distortion, which is usually most intense at the end of indexed time-series (Melvin and Briffa 2008). However, the novel signal-free detrending technique is considered to minimize such biases (Melvin and Briffa 2008; Fang et al. 2012).

Here, we describe growth trends and climate responses of Norway spruce within its natural elevational distribution range in the mountain regions of East-Central Europe (the Sudetes and Babia Góra Mts. in southern Poland, northern Czech Republic and Slovakia). We used a uniform sampling design for all sites. Similar relative positions of sampling sites towards the common upper limit of tree growth (timberline) were maintained, and tree-ring chronologies were built from comparable numbers of samples with similar age representation at each elevational belt within the spruce montane forests. Differences in growth patterns and growth–climate relationships were assessed along elevational gradients. We expected that: (1) the elevational transitions between temperature-limited tree growth and growth with a mixed climatic signal will increase with the higher position of alpine timberline towards the east; and (2) the amplitude of decadal-scale growth variability (herein called as "medium-frequency") will increase with elevation because of a stronger temperature effect on tree ring formation.

Data and methods

Geographical setting

The focal area for our study is the mountainous area in East-Central Europe, i.e. the region situated at 50°N latitude and between 15° and 19°E longitude (Fig. 1). The study region comprises medium-elevation (between 1491 and 1725 m) ranges including crystalline mountains (Krkonoše Mts., Jeseníky Mts.) of the Sudetes and flysch areas (Babia Góra Mts.) of the western Carpathians. Norway spruce dominates montane forests up to timberline (Chytrý 2013).

Climate is cold and humid with annual precipitation totals ranging from 1200 mm in the Jeseníky Mts. to 1500 and 1800 mm at summits of the Babia Góra and Krkonoše

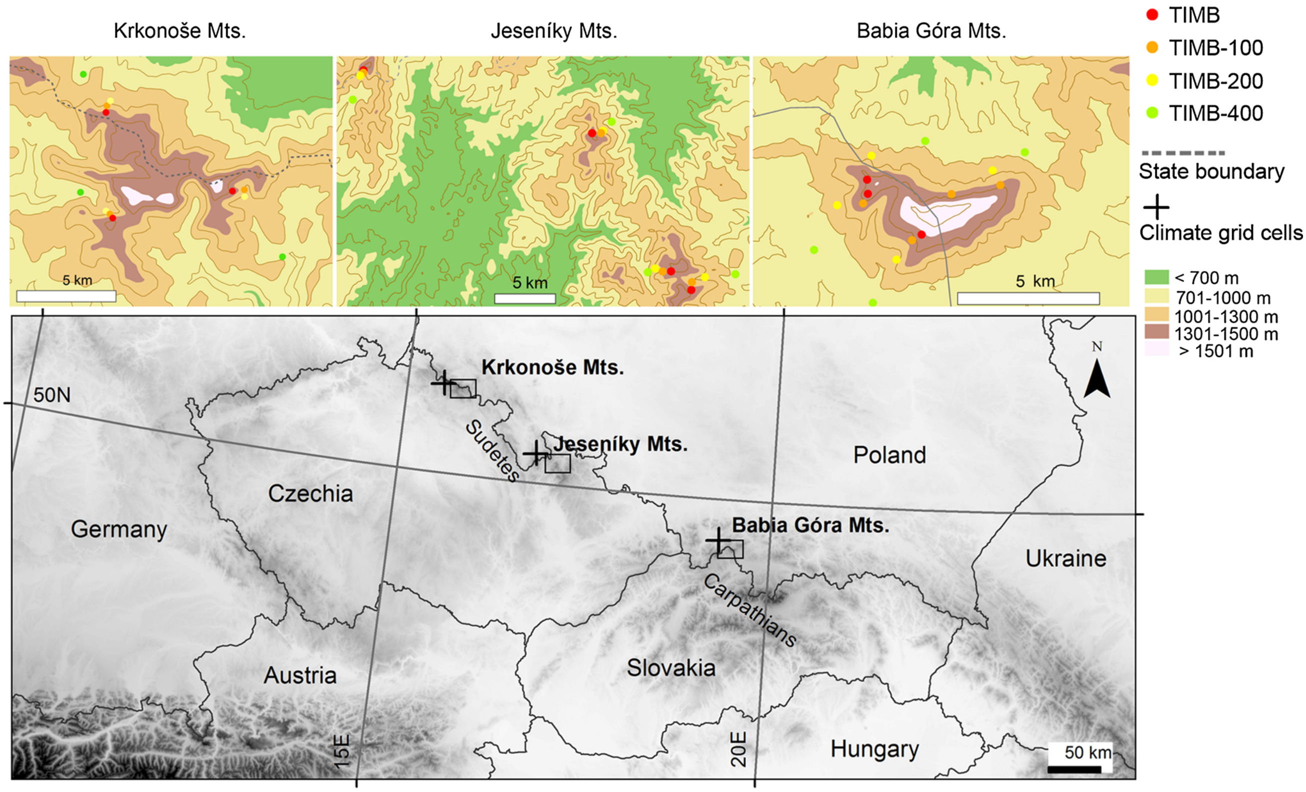


Fig. 1 Location of the study area. *Rectangles* in the main map delimit insets with detailed maps of studied regions (*above*). Elevation contours are 200 m steps. "TIMB-100" denotes elevation belt timberline-100 m, etc

mountain ranges, respectively (Kwiatkowski 1982; Migala 2005; Obrebska-Starkel 2004). Soils of the montane forests are mostly podzols, acidic nutrient-poor cambisols, and rankers (Tomášek 1995; Granec and Šurina 1999).

The alpine timberline ranges from 1300 m in the Krkonoše Mts. to ca. 1450 m in the Babia Góra Mts. (Treml and Chuman 2015; Czajka et al. 2015). The uppermost margins of the montane forest zone contain remnant forests of natural origin (logged occasionally in the past), whereas managed spruce plantations dominate lower elevations. During the 1970s and 1980s, forests of the study area were affected by acid pollution resulting in growth depression, which was most pronounced toward the west (Kroupová 2002).

Tree-ring sampling and processing

Increment cores from living co-dominant or dominant Norway spruces were collected between 900 and 1450 m a.s.l. at 40 locations, comprising 16 sites in the Jeseníky Mts, 12 in the Krkonoše Mts and 15 in the Babia Góra Mts. (Fig. 1). Samples were collected at prescribed elevations relative to the timberline in the zone spanning 400–500 elevation meters [timberline, 100, 200 and 400–500 m below the timberline (Table 1)]. The sites were selected to represent stands with diverse age structures and without visible recent human intervention (e.g., no evidence of logging or grazing); however, at low-elevation sites, planted stands were also sampled. Each elevation belt in each mountain range contained at least three sites covering different slope aspects to account for potential aspect- and site-specific effects (Table 1). Canopy cover at sampled sites increased from the timberline to the timberline-100 m belt, beyond which canopy cover remained relatively constant. Additionally, we made an effort to obtain homogenous datasets in terms of age distributions of samples and balanced representation of individual sites (Fig. 2; Table 1). Fieldwork was conducted between 2010 and 2012.

Cores were extracted at breast height (~1.3 m above the ground), and from most trees two cores were collected to avoid eccentricity and compression wood due to slope inclination or prevailing wind direction. Cores were prepared using standard dendrochronological methods (Stokes and Smiley 1996). Tree-ring width (TRW) was measured to the nearest 0.01 mm with a positioning table. Successfully cross-dated series were included in the final dataset.

In order to remove both age-related trends in TRW and other non-climatic noise from the raw TRW, we performed individual-based detrending using splines with a 66 %

Table 1 Basic characteristics of study sites and tree ring chronologies

Region	Elevation belt	Elevation (m a.s.l.)	Number of trees	Number of sites	Site aspects	Average tree height (m)	Chronology length with EPS > 0.85	Average ring width (mm)	Average age (±SD)
Krkonoše	Timberline	1300	51	3	NW, N, SE	9	176	1.34	125 ± 34
	Timberline-100 m	1200	43	3	NW, N, SE	14	128	1.50	128 ± 33
	Timberline-200 m	1100	43	3	NW, N, SE	18	142	1.56	107 ± 34
	Timberline-400 m	900	45	3	NW, N, SE	21	108	2.28	90 ± 25
Jeseníky	Timberline	1350	47	4	S, NE, NE, SW	10	147	1.32	117 ± 33
	Timberline-100 m	1200	49	4	S, NE, NE, SW	17	162	1.69	139 ± 25
	Timberline-200 m	1100	50	4	S, NE, NE, SW	22	142	1.90	137 ± 26
	Timberline-400 m	900	47	4	S, NE, NE, SW	23	122	2.05	114 ± 25
Babia Góra	Timberline	1450	48	3	S, SW, W	11	128	1.27	134 ± 27
	Timberline-100 m	1350	52	4	S, SW, N, NW	18	113	1.28	125 ± 30
	Timberline-200 m	1200	52	4	S, SW, N, NW	22	128	1.82	122 ± 31
	Timberline-400 m	950	46	4	S, SW, N, NW	24	113	1.88	103 ± 25

variability cut-off at 90 years (i.e. approximate mean series length at each site) (Treml et al. 2012). Two types of TRW chronologies were produced. First, to emphasize high-frequency variability, the autocorrelation was removed and residual chronologies were created (Cook 1985). Residual chronologies were used for determination of growth–climate responses. Second, to emphasize medium-frequency variability, signal-free standard chronologies were created (Melvin and Briffa 2008). Signal-free standard chronologies were used to compare growth trends. Both chronology types were truncated at a minimum sample replication of at least five series.

Differences in TRW, mean sensitivity and tree age between elevation belts and between mountain ranges were tested using ANOVA and post hoc tests. Similarity in residual TRW chronologies was evaluated through hierarchical clustering based on Ward's method (Ward 1963). In addition, principal component analysis for both residual and standard chronologies was applied to quantitatively assess main variance components (principal components) in TRW chronologies.

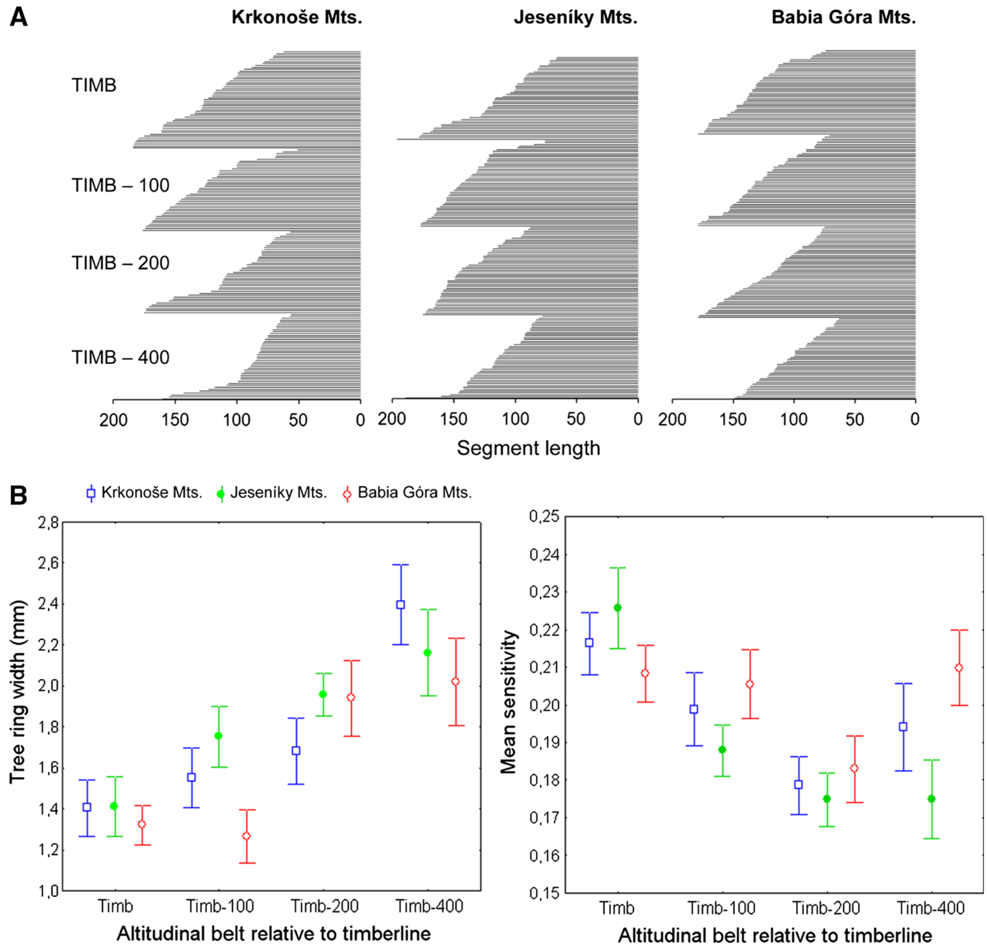
Medium-frequency growth variability was measured using the standard deviation (SD) of signal-free chronologies, which were filtered using a 20-year low-pass Gaussian filter (Büntgen et al. 2010). Breakpoints in linear trends of standard chronologies (i.e. the points where regression coefficients change) were identified using the *R* package strucchange (Zeileis et al. 2003, 2015), minimum segment length was set to 20 years. Further, slopes of linear trends were determined over fixed intervals (1920–1950, 1950–1980 and 1980–2010), which approximate main depressions and culminations of standard chronologies. Statistical significance of trends was evaluated through Mann–Kendall test (Chatfield 2004).

Growth–climate relationships

To assess growth–climate relationships of trees in each elevation belt, we calculated response functions of residual chronologies and climatic variables with monthly resolution. Monthly temperature means and monthly precipitation sums were obtained from CRU TS series with 0.5° resolution (Harris et al. 2014). Climatic data for the following grid cells were used: 50.5°–51.0°N, 15.5°–16.0°E (Krkonoše); 50.0°–50.5°N, 16.5°–17.0°E (Jeseníky) and 49.5°–50.0°N, 19.0°–19.5°E (Babia Góra). The response function was calculated over the period of common overlap for all chronologies and climate data (from 1906 to 2010). In addition, moving response functions were computed over a 68-year window, which was the shortest possible window, when using two climatic variables (Biondi and Waikul 2004). For the sake of simplicity, only moving response functions of TRW to the most influential monthly climatic variables and variables with significant trends are presented. Analyses were calculated for the period beginning in May of the year preceding ring formation to the September of the ring-formation year (Fritts 1976). Growth–climate responses were analysed using DENDROCLIM 2002 (Biondi and Waikul 2004). Significance of the linear trends in climatic data was tested using Mann–Kendall test.

Further, Pearsońs correlations with probabilities derived from normal distribution were computed for the seasonal temperature means. The overall amount of variability in TRW chronologies explained by temperatures and precipitation was calculated through multiple stepwise regressions. Captured variability was measured using R^2. In order to account for multicollinearity of explanatory climatic variables, principal component analysis was used to

Fig. 2 **a** Age distribution ("TIMB-100" denotes elevation belt timberline-100 m, etc.); **b** tree ring widths and mean sensitivity, with *vertical bars* denoting confidence intervals (0.95) and *middle* points indicating mean values. Mean sensitivity refers to raw TRW series



simplify the data structure, and principal components were used in regression models.

To assess coherency in trends of TRW chronologies and climate, correlations between low-pass filtered TRW chronologies and temperature and precipitation principal components were computed. Statistical significance of correlations was adjusted for effective sample size of strongly autocorrelated time series (Chatfield 2004).

Results

Growth patterns

We constructed 12 TRW chronologies representing the three regions and four altitudinal belts covering the natural range of montane Norway spruce. Chronologies are based on growth curves from 573 trees and 1056 tree-ring series (Table 1). The common overlapping interval of chronologies with sufficient expressed population signal spans from 1906 to 2010. Age classes from 70 to 180 years were represented in all chronologies. Although age representation is fairly equal (Table 1, Fig. 2a), there are some differences between elevation belts and regions. The lowest elevation belts tended to be represented by younger trees than the upper elevation belts (in Babia Góra and Krkonoše, $p < 0.05$). In the Jeseníky Mts., both timberline trees and trees from the lowest elevation belt are younger than trees from the medium elevation belts ($p < 0.05$). In all regions, TRW decreased with increasing elevation and were consistently different between timberline trees and the two lowest belts ($p < 0.05$). The mean sensitivity of tree ring series was high at both ends of the transects, i.e. at timberline and in the lowest belts, and low in medium elevation belts (Fig. 2b).

Residual TRW chronologies covering the common period between 1906 and 2010 clustered into two main groups. The first consisted of all the lowest elevation belts and the timberline-200 m belt from Babia Góra; the other consisted of the sites situated in higher elevations (Fig. 3a). The second group was divided into two further groups: chronologies from the Krkonoše Mts., and chronologies from the Jeseníky and Babia Góra Mts. The first principal component (PC) captures 68 % of variability in residual chronologies (Fig. 3b). All chronologies are significantly correlated only with PC1, except the lowermost elevation

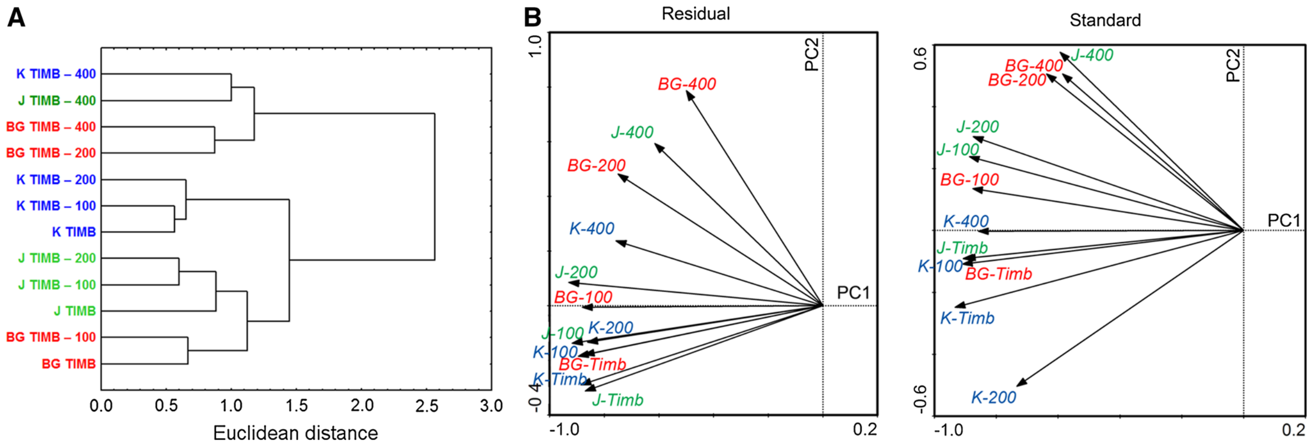


Fig. 3 **a** Hierarchical clusters indicating similarity of TRW chronologies. Chronology codes: *K* Krkonoše (*blue*), *J* Jeseníky (*green*), *BG* Babia Góra (*red*); *TIMB* timberline; −100, 200, 400-corresponding elevation belts below timberline. **b** Ordination *plots* of principal component analysis for residual and standard chronologies

belt in all mountain ranges and Babia Góra-200 m belt, which have high loadings also at PC2 (capturing 12 % of data variability). For standard chronologies, the first principal component captures 70 % of data variability and most chronologies again showed their highest loadings at PC1 (Fig. 3b). PC2 (covering 9 % of variability) is correlated with the lowermost chronologies from Jeseníky and Babia Góra (−200 m belt). Jeseníky-400 m, Krkonoše-400 m and Krkonoše -200 m belts have also high loadings at PC3 (5 % of variance explained).

Growth trends varied substantially among the elevational belts and longitudes (Fig. 4a). Medium-frequency variation of smoothed standard chronologies was highest at timberline (mean SD = 0.169), medium in mid-elevation belts (mean SD = 0.109, 0.114 for timberline-100 m and timberline-200 m belts) and lowest at the timberline-400 m belt (mean SD = 0.098). In Jeseníky and Babia Góra the timberline and lowermost elevation belt chronologies revealed two trend breakpoints, the remaining elevation belts had only one trend breakpoint (Fig. 4a). Chronologies from the Krkonoše Mts. showed two or three trend breakpoints at three lower elevation belts and at timberline, respectively. For all chronologies, the first trend breakpoint was detected between 1925 and 1933. The second was detected in 1972 or 1973 in Jeseníky and Babia Góra, and in 1978 and 1979 in Krkonoše and lowermost elevation belts of the remaining areas. Slopes of linear trends over fixed 30 year intervals approximating sections between main depressions and culminations were statistically significant only at timberline (Fig. 4b). In the last interval (1980–2010), increasing slopes of all chronologies were significant with the exception of the lowermost elevation belt of Babia Góra (Fig. 4b).

Whereas 20th century and contemporary tree growth at timberline-400 m were similar, the contemporary growth rates of trees in the remaining elevation belts were unprecedented since 1900. In contrast to the Jeseníky and the Babia Góra Mts., growth depression in the 1970s was pronounced at each altitudinal level in the Krkonoše Mts.

Growth–climate response

Radial increments of trees growing at the three highest elevation belts were affected primarily by June and July temperatures (Fig. 5). June temperatures showed the highest loadings, attaining 0.32 for timberline and timberline-100 m elevation belts. June temperature loadings increased towards the east. For July temperature, the elevation belts with the highest loadings shifted down from timberline in the Krkonoše Mts. to the timberline-100 m belt in the Jeseníky Mts. and to the timberline-200 m belt in the Babia Góra Mts. Timberline-400 m chronologies did not display any significant response to June and July temperatures, and the response of the timberline-200 m chronology from the Babia Góra Mts. was related only to July temperature. Aside from summer temperatures, tree growth in the three highest elevational belts was significantly affected by temperature of the preceding October, particularly in the Krkonoše and Jeseníky Mts., where October temperature loadings reached 0.24 and 0.28, respectively (Fig. 5). Correlations of TRW with seasonal temperature means were highest in the two uppermost elevation belts and radial growth responded primarily to June–July temperature means. Correlation coefficients were 0.50 in Krkonoše timberline, 0.57 in Jeseníky timberline-100 m and 0.53 in Babia Góra timberline belt.

The response of radial growth to summer precipitation was significant at the lowest zone (Jeseníky, Babia Góra) or the timberline-200 m belt (Krkonoše) (Fig. 5). Regardless of elevational position, tree growth was positively

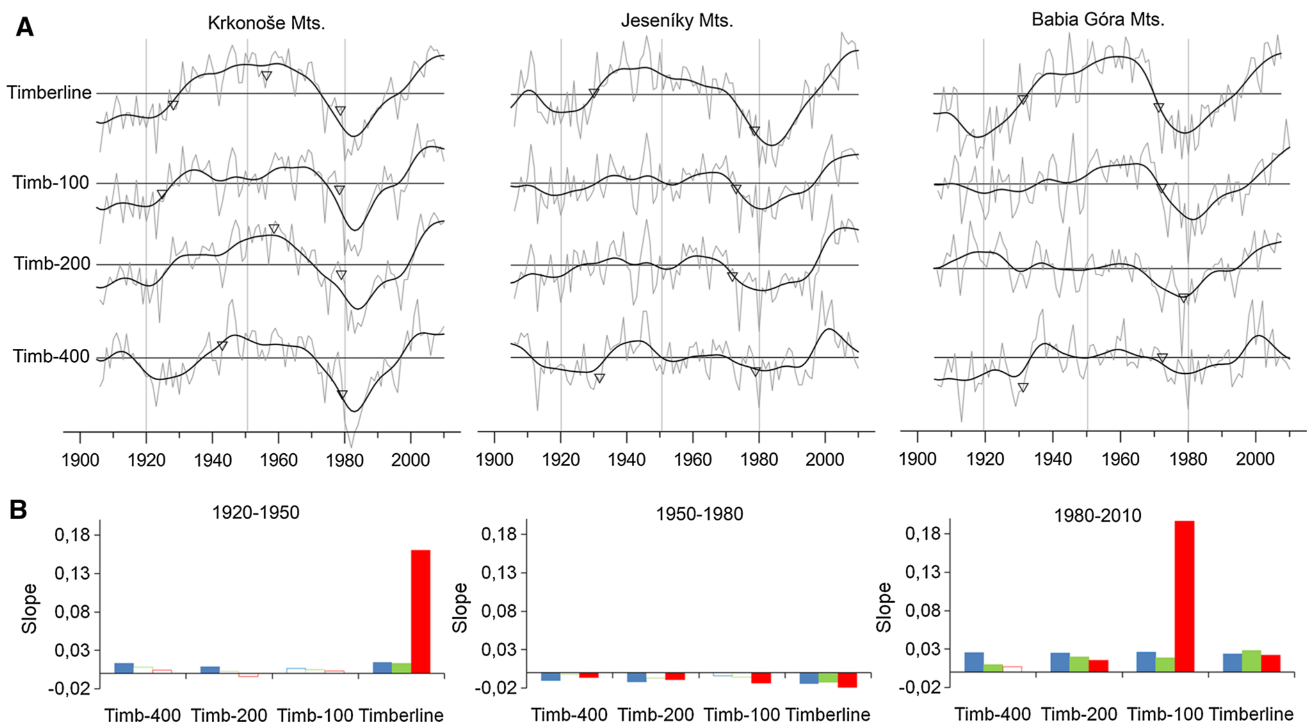


Fig. 4 **a** Growth trends based on signal-free standard chronologies filtered by a 20-year, low-pass Gaussian filter. Triangles indicate breakpoints in linear trends. **b** Slopes of linear trends over fixed periods determined from standard TRW chronologies. *Full columns* denote statistically significant trends based on the Mann–Kendall test. *Colors* are as follows: *Blue* Krkonoše, *Green* Jeseníky, *Red* Babia Góra

influenced by February precipitation, attaining loadings of 0.15–0.26, with its strongest influence in the eastern part of the region.

The total variance explained by climatic variables (simplified in principal components) increased with increasing elevation (Table 2). However, this growth–climate response pattern was more complex in the Jeseníky Mts., where the greatest proportion of variance attributed to climate variables was captured in the chronology from the timberline-100 m belt. The highest amount of variance attributed to climate variables (up to 54 % of variance explained) was in the timberline belt of Babia Góra. Babia Góra TRW chronologies tended to be driven by climate more than those from western locations.

Analysis of the moving response functions (Fig. 6a) indicated that in the Krkonoše Mts. the effect of preceding October temperatures on radial growth was significant only in the first half of the study period in nearly all elevation belts. In addition, the response to early spring temperatures gradually transitioned from negative to positive.

In the Jeseníky Mts., there was an increasing effect of March precipitation in the timberline-100 m and timberline-200 m belts (Fig. 6a). The three uppermost elevational belts exhibited obvious trends of increasing responses to summer precipitation and early spring temperature in the second half of the 20th century. In the same period, the effect of the preceding October temperatures became non-significant in the timberline zone.

In the Babia Góra Mts., tree growth responded positively to April temperatures after the 1950s–1960s except in the lowermost zone, where TRW response to April temperatures was stable and strong across time. In contrast, the positive effect of preceding October temperatures gradually diminished in the same period (timberline-100 m). In the lowermost zone of the Babia Góra Mts, the negative effect of September temperatures in the year preceding ring formation emerged during the last 40 years (Fig. 6a). Response functions of remaining monthly climatic variables either were not significant over the study period or did not show any trend.

Trends of those climatic variables that largely affect radial growth involve relatively steep slopes of increasing April temperatures, stable or increasing trends of June temperatures and increasing October temperatures (Fig. 6b). The largest regional differences were determined for trends in July precipitation, which has been increasing in Krkonoše and had negative (though insignificant) slopes in Jeseníky and in Babia Góra.

Low-pass filtered chronologies across all elevation belts were significantly correlated with smoothed temperature PCs in the Krkonoše and Jeseníky Mts (PC2 in both regions, Pearson *r* ranges from 0.66 for GM timberline-400

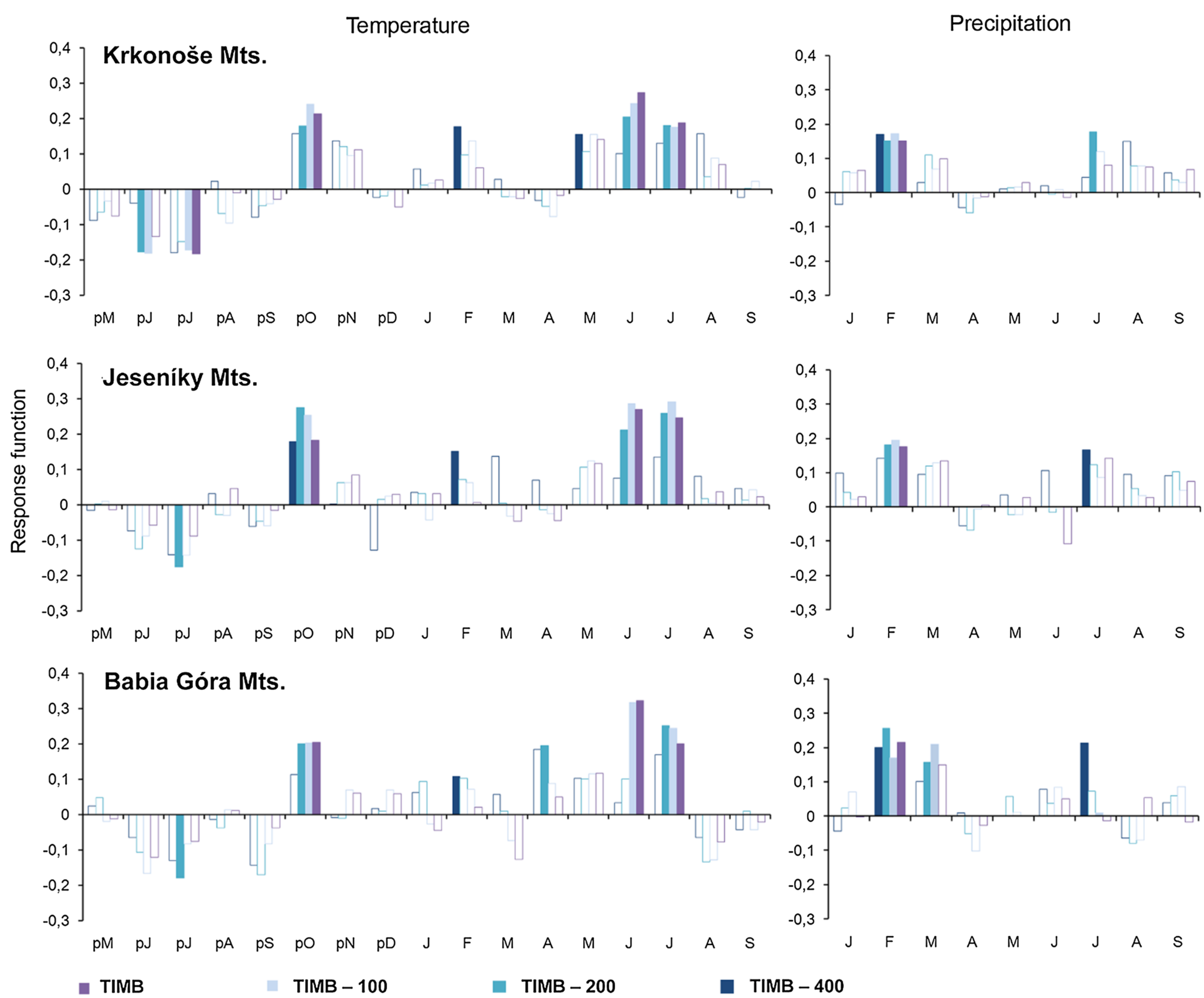


Fig. 5 Growth–climate responses as indicated by response function analysis. *Full bars* denote statistically significant response functions. Only months of the year of ring formation are depicted for precipitation because of the absence of statistically significant responses for the year preceding ring formation

Table 2 Variance in TRW chronologies explained by climate, as indicated by R^2

Elevation belt	Krkonoše Mts.	Jeseníky Mts.	Babia Góra Mts.
Timberline	0.46	0.44	0.54
Timberline-100	0.45	0.52	0.52
Timberline-200	0.37	0.50	0.46
Timberline-400	0.34	0.38	0.42

to $r = 0.83$ for Jes timberline-100) (Fig. 7). In Babia Góra, the coherency between radial growth and temperature PC1 was significant only for the uppermost ($r = -0.76$) and the lowermost elevation belt ($r = -0.73$). Statistically significant correlations exceeded the threshold of ($\pm$) 0.65 at $\alpha = 0.1$. Temperature PCs represented between 24 and 34 % of temperature variability and were mainly correlated with summer temperatures. In all regions and elevation belts, smoothed TRW chronologies were not significantly correlated with precipitation PCs 1 and 2 covering the major part of precipitation variability. Only precipitation PCs 3 showed significant correlation with chronologies from the lowermost elevation belts in the Jeseníky ($r = -0.65$) and Babia Góra Mts. ($r = 0.66$) (Fig. 7), however correlations were at the limit of statistical significance at $\alpha = 0.1$. Precipitation PCs 3 represented 15 and 13 % of precipitation variability for the Jeseníky and Babia Góra Mts. respectively (PC3 in both regions). March, May, August and September precipitation had highest loadings in PC3 both in the Jeseníky and Babia Góra Mts.

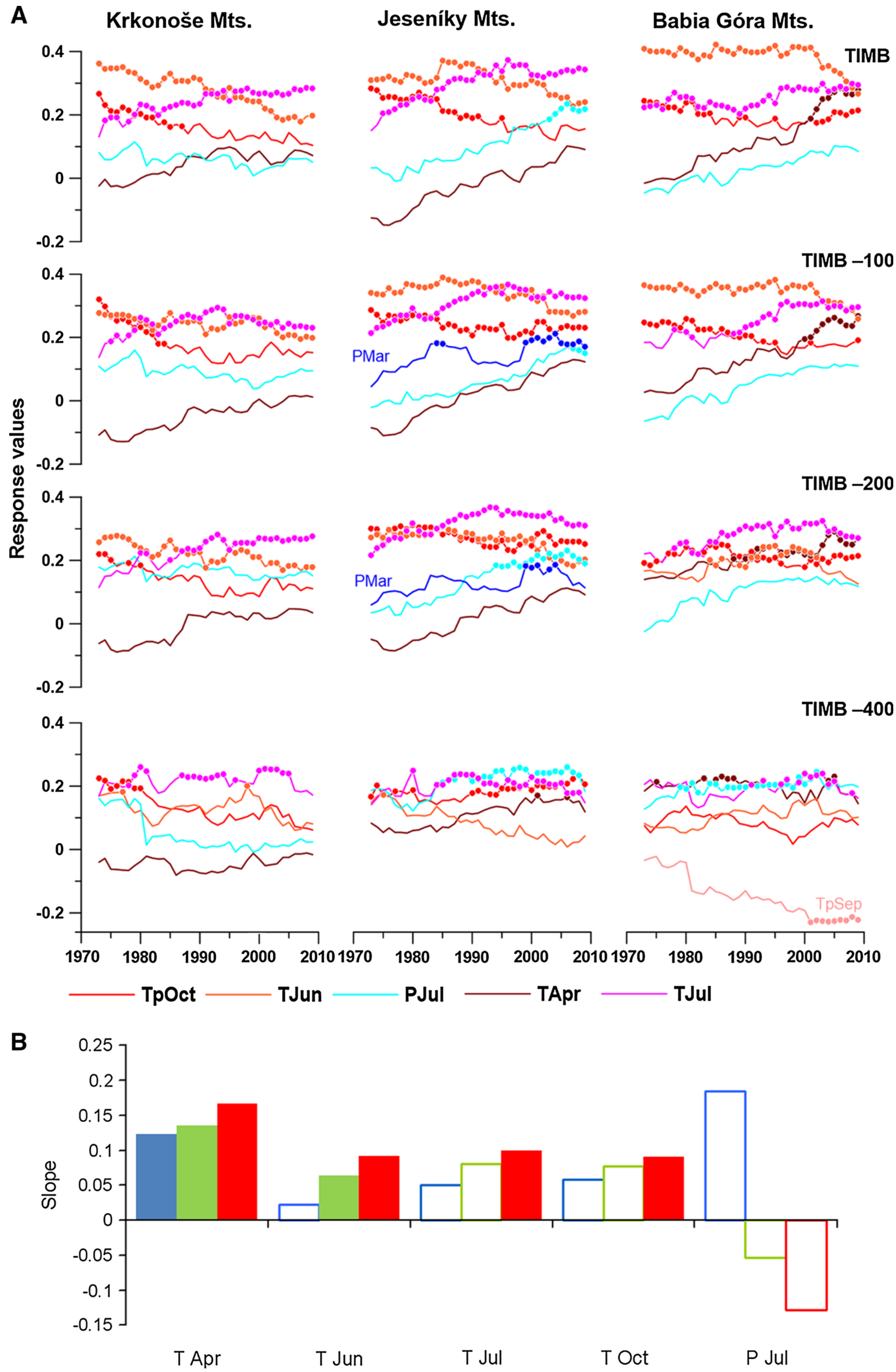


Fig. 6 **a** Moving response functions showing the response of TRW to climatic variables. *Dotted lines* indicate statistically significant responses. **b** Trends in selected climatic variables over the period 1906–2010. Note that trends for temperatures are ×10 exaggerated. *Full columns* denote statistically significant trends. *Colors* are as follows: *Blue* Krkonoše, *Green* Jeseníky, *Red* Babia Góra. *TL* timberline, *TpOct* temperature in October of the year preceding tree ring formation, *TpSep* temperature in September of the year preceding tree ring formation, *TJun* June temperature, *TJul* July temperature, *TApr* April temperature, *PJul* July precipitation

Discussion

In East-Central Europe, the elevational stratification of Norway spruce TRW chronologies capturing high-frequency variability is more important than regional stratification, with distinctly different growth patterns in the upper montane belt (ca. 200-m-wide zone below timberline) and the lower montane belt (timberline-400 m). A similar general pattern, i.e. differences between tree growth in the upper and lower montane belts has been detected in the Tatra Mts. (Savva et al. 2006; Büntgen et al. 2007), Eastern Carpathians (Sidor et al. 2015), and Austrian Alps

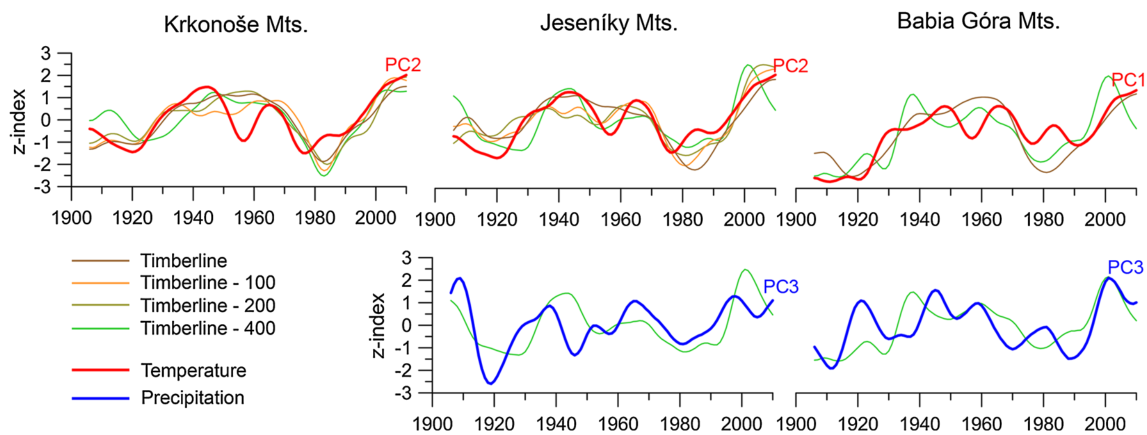


Fig. 7 Coherency between low-pass filtered TRW chronologies and temperature or precipitation principal components. Significantly correlated chronologies and principal components are displayed only. Note that for the Krkonoše Mts., there were no significant correlations between TRW chronologies and precipitation principal components. Time series were standardized to have unit variance and zero mean. To make comparison of trends easier, temperature PC1 for Babia Góra and precipitation PC3 for Jeseníky Mts. were multiplied by −1, because these PCs were negatively correlated with chronologies

(Leal et al. 2007). Our study demonstrates that this differentiation has its consequences in growth trends and medium-frequency growth variability, which vary considerably between the zone adjacent to timberline and the lower-montane belt. We also found that if medium-frequency growth variability is considered, the difference between lowermost TRW chronologies and chronologies adjacent to timberline is retained, however the group of lowermost chronologies is more heterogeneous than it was observed for residual chronologies capturing high-frequency growth variability. This heterogeneity probably reflects differences in trends of climatic variables affecting growth in the western and eastern parts of the study area–particularly April temperatures and July precipitation.

The lowest elevation chronologies showed relatively low medium-frequency variability, the smallest growth increase since the 1980s, and a decreasing or stable growth trend in the 2000s. In contrast, the chronologies from the 200 m zone adjacent to timberline revealed high medium-frequency variability and rapid growth increase since the 1980s. Recent growth rates of these high-elevation trees appear to be unprecedented in the century-long context. Both medium-frequency variability and growth increase were greatest at timberline. Our findings are similar to those for *Pinus longaeva* in western North America (Salzer et al. 2009), where recent growth rates for timberline trees have accelerated from historical rates. In contrast, in the Northern Alps, i.e. the region situated nearby our study area, a greater positive growth change in 1990s and 2000s was reported from the lower montane belt than from the timberline zone (Hartl-Meier et al. 2014a, b). These differences demonstrate high regional variability in growth responses to recent warming that might be a consequence of distinct regional climatic trends and, to some extent, might also result from different approaches used to compare growth trends. For instance, Hartl-Meier et al. (2014b) compared growth trends across a broader area involving regions with increasing and decreasing precipitation. If a reaction of trees to drought is considered in isolation, the interpretation from the northern Alps is very similar to that from eastern part of Central Europe. That is, trees from the lower montane zone react to drought episodes, whereas trees in elevation belts adjacent to timberline reveal positive growth response to growing seasons with high summer temperatures. Anyway, montane spruce forests in Central Europe revealed radial growth increase since 1980s with varying magnitude depending on elevation (Hasenauer et al. 1999; Hartl-Meier et al. 2014a, b).

In line with growth trends, the effects of single climatic variables on radial growth of Norway spruce also exhibited both elevational and longitudinal differences. From timberline-200 m upwards, radial growth corresponded primarily with June–July temperatures and temperatures in the preceding October, whereas trees in the lowest elevational zone (timberline-400 m) responded to both temperature and precipitation. June–July is the period of most intense cell enlargement (Cuny et al. 2014), whereas the positive effect of preceding October temperatures is mediated by carbon storage (Oberhuber 2004). We also observed that the responses of radial growth to October temperatures in the year preceding ring formation decreased over the last century in all timberline zones. This may be due to a warmer climate, where timberline trees are no longer limited by the amount of resources stored at the end of the growing season (Treml et al. 2012).

The only precipitation variable that consistently affected tree growth was February precipitation. Positive responses to February precipitation have also been reported from the broader region along the Czech/Polish border for both *P. abies* and *Pinus sylvestris* from medium elevations (Feliksik 1993; Wilczyński and Skrzyszewski 2002; Rybníček et al. 2009). Büntgen et al. (2007) reported a significant effect of February–April precipitation on tree growth in the Tatry Mts., and attribute this positive effect to the water supply at the beginning of the growing season. Others ascribe the positive influence of February precipitation to the protective effect of the snow pack, which prevents soil from freezing and decreases the risk of winter desiccation (Rybníček et al. 2009) and/or fine-roots dieback (Tierney et al. 2001).

The amount of growth variability explained by climatic variables increased with elevation and was generally highest at timberline, associated with nearly exclusively temperature-limited growth of timberline trees (Körner 2012). However, the amount of explained variability within a given elevation zone also increased towards the east. The amount of climatically explained variability at Babia Góra was ~54 % at timberline and ~46 % in the timberline-200 m zone, similar to the Vysoké Tatry Mts. (20°E) (Savva et al. 2006). Weaker climatic forcing of tree growth in the western part of the longitudinal transect is probably attributable to high air pollution loading during the 1970s and 1980s, with the strongest deposition rates in the west (Kroupová 2002). This phenomenon was also manifested in the somewhat exceptional medium-frequency variability exhibited in the lowest-elevation chronology in Krkonoše, which is attributable to the deep growth depression in the 1970s and 1980s (Kolář et al. 2015).

We are aware that changing stand structure over time could affect detected growth trends (Kimmins 2004). However, growth trends were homogenous across different sites, so it is improbable that possible past forest management activities or disturbances heavily influenced our results or interpretation. Whereas past management activities could not be excluded in most lowermost stands (i.e. timberline-400 m), some timberline stands were affected by canopy opening due to increasing mortality in the 1970s and 1980s as a consequence of acid rain pollution (Kolář et al. 2015). These stands had been mostly open before this mortality event, and is the reason why the effect of canopy opening on substantial growth increase between the 1980 and 2000s was not likely of high importance.

Based on the observed growth–climate relationships and growth trends, we suggest that the zone where Norway spruce growth has benefited from recent temperature rise covers a ~200- to 300-m-wide altitudinal belt below timberline. Rising summer temperatures are the most important drivers of enhanced high-elevation tree growth in East-Central Europe, where tree-ring patterns are well correlated with summer temperatures and both station and gridded temperature series show the highest summer temperatures to have occurred from the 1990s onwards (Glowicki 1997; Harris et al. 2014). At lower elevations stable or even decreasing radial growth in the most recent period demonstrates an ambiguous or slight negative effect of recent climatic trends on tree growth. This overall picture was also manifested in medium-frequency coherency between radial growth and climate. TRW chronologies from upper elevation belts corresponded exclusively with temperature trends, whereas both temperature and precipitation trends were reflected in TRW chronologies from the lowermost elevation belts in the Jeseníky and Babia Góra Mts.

Using results from this study and from adjacent regions of Central Europe, one could map the elevational positions of transitions in growth–climate responses of Norway spruce. Towards the east, the lower limit of the elevation zone with a clear summer temperature signal increases from about 1100 m in the Sudetes to 1350 m in Babia Góra. In the eastern portion of our longitudinal transect, the elevational position of the zone with a pure temperature signal is approximately the same as in the area of the Vysoké Tatry Mts., located about 50 km eastwards from Babia Góra. In this area, Büntgen et al. (2007) and Savva et al. (2006) showed a consistently strong June-July temperature signal of Norway spruce only at elevations above 1350 m. South from our longitudinal transect, the nearest pronounced elevational gradients are in the Bavarian Forest and in the Northern Alps. In both these regions, Norway spruce chronologies with clear summer temperature signals occur above ca. 1300–1400 m (Wilson and Hopfmueller 2001; Leal et al. 2007; Hartl-Meier et al. 2014a). Across Central Europe, the zone with purely temperature-limited tree growth thus increases from ca. 1100 m at the western margins of the Sudetes (50°N, 15°E) up to 1350 m towards the east at the 20°E and up to 1400 m towards the south at the 47°N. Norway spruce from this elevation zone thus provides a suitable basis for dendroclimatic reconstructions.

The transition between the zone of mixed climatic signal and the zone where tree growth is influenced by precipitation also increases in elevation towards the east. In the Krkonoše Mts. there are rather high correlations with temperatures at 900 m, whereas summer precipitation most strongly affected radial growth of trees (and the effect of summer temperatures was negligible) at 900 m in the Babia Góra Mts. This trend in the west-east direction is supported by a mixed climatic signal in Norway spruce chronologies from the 800–900 m altitudinal belt in the central Sudetes (17°E, Rybníček et al. 2009) and a precipitation-dominated climatic signal in the westernmost Carpathians at 800 m (18°E, Rybníček et al. 2010). Toward the south, there is a prevailing precipitation signal below 950 m in the Northern Alps (Hartl-Meier et al. 2014a) and below 800 m in the Bavarian Forest (Wilson and Hopfmueller 2001).

Similar to temporal changes in growth trends, we observed shifts in growth–climate responses. Aside from the effect of preceding October temperatures, the other climate-response shifts were regionally specific and matched well with specific trends in climatic variables. These consisted of increased sensitivity to early growing season temperatures (Babia Góra) and also some indirect indications of drought influence, such as increasing positive responses to precipitation and negative responses to summer and autumn temperatures in the east (Jeseníky and Babia Góra). The increasing tendency of drought effects on growth corresponds with decreasing July precipitation in Jeseníky and Babia Góra areas. The increasing effect of early growing-season temperatures is typical for high-elevation tree growth in the broader region of the Western Carpathians (Büntgen et al. 2007) and, as we found, might be attributed to the increasing April temperatures over the last century and resulting earlier growing season beginning.

Our approach considers timberline as a starting upper point of transects, where temperatures regardless of region identically limit tree growth. As such, the degree of tree-growth limitation was approximately the same in all the study areas, with mean TRW of $\sim$1.3 mm. This value is similar to the ring widths from nearby Norway spruce timberlines (e.g. High Tatras Savva et al. 2006; Büntgen et al. 2007; Eastern Carpathians Sidor et al. 2015) suggesting comparable climatic forcing of growth rates at timberlines in Central and Eastern Europe.

Conclusions

Along a 600 km longitudinal transect in East-Central European mountain ranges, we observed substantial differentiation in tree growth patterns for Norway spruce as a function of elevation (i.e. distance to timberline). This differentiation was expressed both in the growth responses to climate and in growth rates and trends. While temperature-limited trees in the upper montane zone adjacent to timberline exhibited high medium-frequency growth variability and a strong increasing growth trend since the 1980s, trees in the lower-montane zone (400 m below timberline) displayed relatively low medium-frequency variability and a stable or slight decreasing growth trend in the last decade. The transition between temperature-limited trees and trees of mixed climate sensitivity was found to increase in elevation towards the east, which further corresponded to an increase in timberline position. In all regions, temperature-limited trees in the zone adjacent to timberline exhibited unprecedented radial growth in the 1990s and 2000s. Changing climate during the last century resulted in transformation of growth–climate responses of Norway spruce, including weakening of the importance of autumn temperatures for tree growth in the following growing season. Trees in the lower montane zone tended to be more affected by drought in recent decades than before. This was most evident in the eastern part of the study region, where summer precipitation decreased over the last century. Based on our findings, ongoing warming likely results in increasing radial growth rates in the Norway spruce forests adjacent to timberline, whereas the productivity of lower montane forests may either not show distinct trends or even decline.

Author contribution statement T.P. collected and analysed data in the Krkonoše Mts., the Jeseníky Mts. and in the Slovak part of the Babia Góra Mts. and wrote the manuscript; B.C. and R.J.K. collected and analysed data in the Polish part of the Babia Góra Mts. and commented manuscript; U.B. commented on the manuscript; V.T. designed study, collected data, commented and partially wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Divergence of tree growth and summer temperature at treelines in East-Central Europe

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Abstract

There is growing evidence of recent decoupling of tree growth from temperature across cold regions such as northern and mountain treelines. Increasing or diminishing regional coherency in tree growth has also been observed. The temporal and spatial extents of the abovementioned processes are poorly known and their drivers not well understood. Pollution and changing climate have often been discussed as a cause of divergent or convergent growth patterns. We compiled climatic records and robust tree-ring chronologies of *Picea abies* covering 1920-2010 from treelines in four regions in East-Central Europe

(Czech Republic, Poland, Slovakia, 50°N, 15-20°E) that differed in acid pollution loads. Their divergences of radial growth from Jun-Jul temperatures were compared with temperature and pollution trends. We found a period of low intra-regional growth coherency in the 1950s reflecting warmer, less-limiting conditions and land use change. Highly coherent growth in the 1930s, 1970s and 1980s was related to the strong environmental growth-limiting signals of short growing seasons and high acid pollution loads. In all regions, we identified periods with higher (1940-1960s) or lower (1970-1980s) growth than expected based on temperature. In the high-frequency domain, the effect of pollution on growth departure from temperature was limited and detectable exclusively in regions with greatest pollution. In the low-frequency domain, the departures of growth from temperature were caused by combined effects of the changing seasonal window of tree growth sensitivity to climate and pollution load. These results highlight the need to recognize non-stationary noise in the relationship between temperature and tree growth.

Key words: tree-rings; climate change; Picea abies; Norway spruce; warming; growth response

1. Introduction

Mountain forests are crucial carbon sinks (Kurz et al. 2007), making it vital to understand their growth dynamics. Production of stem biomass in mountain forests is primarily affected by competition, disturbance and environmental constraints (Pretzsch et al. 2014). The latter includes climatic variables, among them temperature, which has been showing an almost uniformly increasing trend over recent decades (IPCC 2014). In the temperate zone of Europe, growth responses of mountain forests to increasing temperature have been predominantly positive in terms of radial growth (Leal et al. 2007, Hartl-Meier et al. 2014), with some exceptions from the lower part of the montane forest zone (Ponocná et al. 2016). The strongest positive responses have been reported from treelines (Rolland et al. 1998, Oberhuber 2004, Treml et al. 2015a). However, growth divergence (i.e. decoupling of growth curves from temperature trends) has been observed across many temperate and boreal forests (Wilson et al. 2007, D'Arrigo et al. 2008), even for temperature-limited trees close to their upper or northern limits (D'Arrigo et al. 2004, Wilmking et al. 2005, Galván et al. 2015). Both the degree to which trees are decoupled from climatic forcing and the spatial extent of this phenomenon remains unknown.

In temperature-limited environments, a weakening of the link between radial growth and temperature has been observed in several regions of Canada and Alaska (D'Arrigo et al. 2004, Wilmking et al. 2004), Siberia (Jacoby et al. 2000), the Pyrenees (Galván et al. 2015) and Central Europe (Wilson and Elling 2004). The observed divergences have been attributed to, for instance, the intervention of other climatic limiting factors such as drought in Canadian and Alaskan treeline areas (Barber et al 2000, Lloyd and Fastie 2002). In montane forests of Central Europe, the divergence has been ascribed to the effect of sulfur and nitrogen air pollution (Wilson and Elling 2004, Godek et al. 2009, Rydval and Wilson 2012). It has been suggested that divergence in other areas, particularly boreal forests (D'Arrigo et al. 2007), has been due to the effect of "dimming" (i.e. decrease in incident solar radiation due to increasing concentration of aerosols in the atmosphere). However, Büntgen et al. (2008)

argued that no divergence appears in high-elevation tree-ring chronologies from the Alps, with most treeline chronologies tracking both high and low-frequency temperature variations well.

In our region of interest – Central Europe – growth divergence has been observed not only in mountain but also in lowland tree-ring chronologies. This includes oak chronologies since the 1980s (Dobrovolný et al. 2016, Prokop et al. 2016) and also some silver fir chronologies (Wilson and Elling 2004, Büntgen et al. 2011). Although for fir pollution has been suggested as a probable cause, the sudden decrease in climate sensitivity of oak remains unresolved.

In contrast to observed growth divergence from climatic trends, another general pattern related to changing climatic conditions has recently emerged – increasing convergence in growth patterns within regions (Shestakova et al. 2016). Under increasing environmental stress (e.g. increasing drought severity and/or frequency) tree growth coherency increases as well (Shestakova et al. 2016, Tumajer and Treml 2017). Based on this pattern, assuming that growth of treeline trees is limited by temperature (Körner 2012), their growth coherency should decrease if they are subjected to warming, which may be accompanied by a decrease in strength of the temperature signal in treeline tree-ring chronologies. On the other hand, pollution, as a stressor, could become a driver of convergence in growth patterns.

In this study, we hypothesized that the possible decoupling of tree growth from temperature forcing will be proportional to the pollution load or the degree of warming. We also hypothesized that decoupling will be more obvious in low-frequency variability than in the high-frequency components of time series. This is because the influence of previously negligible or absent variables affecting growth (i.e. pollution, extension of the growing season) are thought to gradually shift the prevailing climate response (D'Arrigo et al. 2008). To test these hypotheses, we built representative tree-ring chronologies, similar in terms of age and site representation, for four treeline areas with a differing air pollution load.

2. Material and Methods

2.1. Geographic setting

The focal area for our study is the mountainous area of East-Central Europe (i.e. the region situated at 50° N latitude and between 15° and 20° E longitude, Fig. 1). The study region comprises crystalline areas of the Krkonoše Mts. (KRK), the Jeseníky Mts. (JES), both belonging to the Bohemian Massif, and flysch, crystalline and limestone massifs of the Carpathians (Babia Góra Mts. - BAB, Nízké Tatry Mts. - NT) with elevations ranging from 1491 to 2056 m a.s.l. Norway spruce (*Picea abies* L. Karst.) dominates montane forests up to the timberline. Prostrate dwarf pine (*Pinus mugo*) is also widespread in the treeline ecotone except at JES. The climate is cold (mean treeline growing season temperature is 6.7°C, Kašpar and Treml 2016) and humid, with annual precipitation totals ranging from 1200 mm in JES to 1500 and 1800 mm on the summits of BAB and KRK, respectively (Kwiatkowski 1982, Obrebska-Starkel 2004, Migała 2005). Soils of the montane forests are mostly podzols, dystric cambisols, and rankers (Tomášek 1995, Granec and Šurina 1999).

The lower limit of the alpine treeline ecotone (i.e. so-called timberline) increases toward the east from 1240 m in KRK to 1320 m in JES, ca. 1370 m in BAB and 1410 m in NT, with maximum timberline positions about 100 m higher than the above-mentioned mean values (Treml and Migoń 2015, Czajka et al. 2015a). Since the second half of the 20th century, treeline ecotones have been gradually advancing upwards as a consequence of land-use change and warming (Weisberg et al. 2013, Czajka et al. 2015b, Treml et al. 2016). During the 1970s and 1980s, forests in the study area were affected by acid pollution resulting in growth suppression and increased mortality (Sander et al. 1996, Rydval and Wilson 2012). The major pollution sources were situated in the boundary region of Germany, Poland and the Czech Republic, which was reflected in a pronounced gradient in reaction to pollution from the western (strongest response) to the eastern part of the study area.

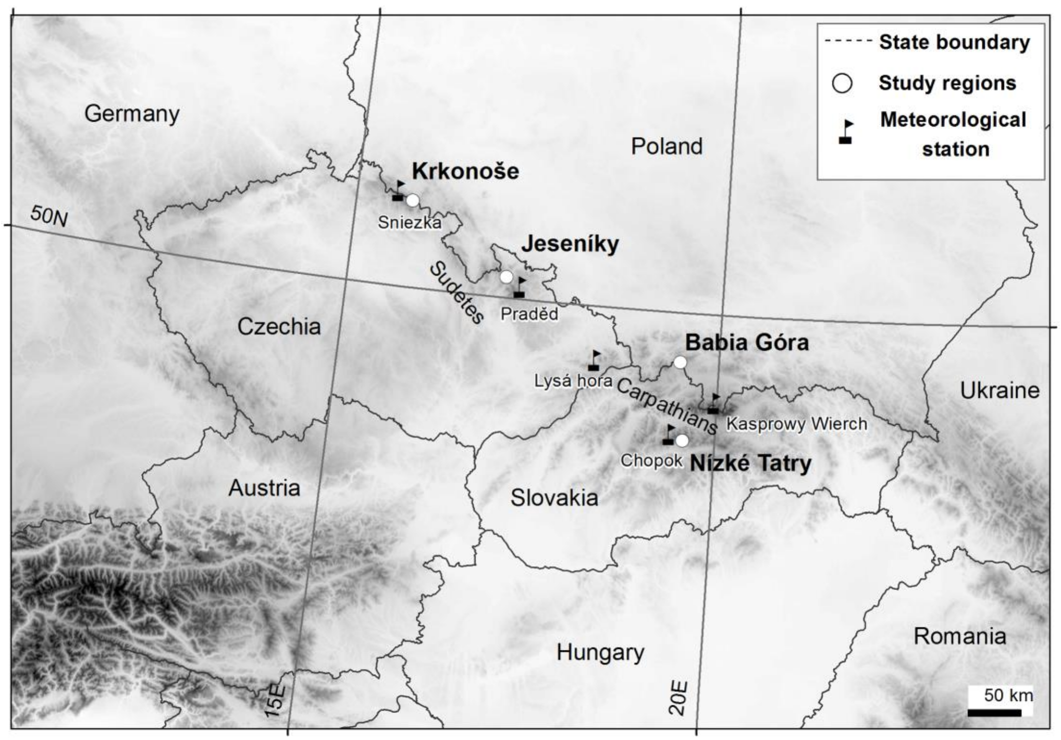

Fig. 1 Locations of study areas: Krkonoše Mts. (KRK), Jeseníky Mts. (JES), Babia Góra Mts. (BAB) and Nízké Tatry Mts. (NT).

2.2. Sampling and sample processing

Increment cores from co-dominant or dominant *P. abies* growing at timberline were collected in KRK, JES, BAB, NT between 2010 and 2012 (Table 1). Each region was represented by two to three sites located on different slope aspects. Mean tree heights were about 10 m. All sites were without visible recent human intervention (e.g., no evidence of recent logging or grazing). Two cores per tree were taken at breast height (approx. 1.3 m above the ground) perpendicular to the slope. Cores were prepared using standard dendrochronological methods (Stokes and Smiley 1996). Core samples were fixed on wooden supports and sanded, and tree-ring width (TRW) was measured to the nearest 0.01 mm with a TimeTable measuring stage (Vienna Institute for Archaeological Science). The minimum sample depth for tree-ring chronologies was 40 trees. Tree-ring chronologies were assembled based on similar age structures among the sites, because differences in age structure might produce differences in growth trends (Carrer and Urbinati 2004, Nehrbass-Ahles et al. 2014). In most regions, the originally extensive sample sets (~60-70 trees) were thus reduced by removing certain age cohorts of trees.

Table 1: Basic site and chronology characteristics.

Region	Number of sites	Site aspects	Site elevation (m ASL)	Number of trees in chronology	Mean age	Chronology start
Krkonoše	3	SW,E	1300	49	122	1830
Jeseníky	3	SW,E	1350	49	108	1836
Babia Góra	2	S,W	1450	40	126	1841
Nízké Tatry	2	S,W	1450	43	119	1823

Each TRW growth curve contains an age trend, which should be removed through tree-ring standardization (Cook and Pederson 2011) prior to the extraction of environmental information. We performed standardization procedures that retain medium to low-frequency variability in growth (i.e. variability in the order of several decades). Since standardization approaches differ in their sensitivity to the age structure of samples (Helama et al. 2004) and in their ability to mitigate the so-called end effect (Melvin and Briffa 2008), we employed two different standardization procedures. First, we performed individual-based detrending using splines with a 66 % variability cut-off at 90 years (i.e. approximate mean series length at each site) (Treml et al. 2012) and signal-free standard chronologies (SF) were created (Melvin and Briffa 2008). Such chronologies allow preservation of medium-frequency growth variability and are free of end effects that may be occur with the application of traditional detrending methods (Melvin and Briffa 2008). These chronologies were created using CRUST software (Melvin and Briffa 2013). Second, basal area increment chronologies (BAI) were constructed (Biondi and Qeadan 2008). BAI detrending was performed in R (package 'dplR') using the BAIin function. BAI chronologies are good at preserving low- to medium-frequency growth variability (Biondi and Qeadan 2008, Hartl-Meier et al. 2014), however, they fail to track environmental signals in periods represented by juvenile growth phases of sampled trees (Sullivan et al. 2016).

2.3. Climate data

For dendroclimatological procedures, climate data with monthly resolution are usually satisfactory (Cook and Kariustis 1990). Treeline tree-ring chronologies in the study area are especially sensitive to June and July temperatures (Ponocná et al. 2016, S1, Suppl.); therefore, the time series of average values of June and July temperatures were used in our analyses. All temperature time series were expressed as departures from mean values over the 1961-1990 reference period. However, we faced two challenges. First, we wanted to obtain temperature series that were as long as possible and, second, we aimed to work with climate series truly representative of high-elevation treeline climates (Weber et al. 1997). Whenever possible, we used station data (WMO 12510 Sniezka – KRK, 1613 m, 1901-2010, Migała et al. 2016). In other cases, we used both long-gridded temperature series from the CRU TS data set (Harris et al. 2014) and available shorter (1961-2010) high-elevation station data from Lysá hora (1322 m, WMO 11787), Kasprowy Wierch (WMO 12650, 1989 m, these stations were representative of BAB) and Chopok (WMO 11916, 2007 m, representative of NT). A significant mismatch in recent temperature trends in CRU and station data was detected in JES (verification station data from local station Praded – 1492 m, 1948-1998) and therefore, the Sniezka temperature was used also for the JES region. Furthermore, BAB CRU Jun-Jul series significantly differed from averaged nearest high-elevation station data (Lysá hora, Kasprowy Wierch) since the mid-1980s. Therefore, a composite time series of Jun-Jul temperature departures from 1961-1990 means was developed using CRU data covering 1901-1961 and mean values from Lysá hora and Kasprowy Wierch representing the period 1961-2010 (see Figure 3).

2.4. Growth-climate coherency

The basic parameters of tree-ring chronologies (TRW, mean sensitivity, first-order autocorrelation) were compared across regions using ANOVA. Coherence in growth trends among individual TRW series within each region was inspected using inter-series correlations (Rbar, Cook and Kariukstis 1990) with a moving window of 21 years length and a 1-year step. For both types of tree-ring chronologies (SF, BAI) and for temperature series, trend breakpoints (i.e., the points where regression coefficients change) were determined using the R package strucchange (Zeileis et al. 2015). For this analysis, the minimum segment length was set to 20 years.

We computed the correlations of TRW and unfiltered Jun-Jul temperature series as well as for high and low-frequency time series. High and low-frequency series were obtained by filtering of original series with high- or low-pass Gaussian filters with a 20-yr window. In addition, moving correlations over 21-yr intervals with a 1-yr step were calculated.

Finally, TRW chronologies and Jun-Jul temperatures were scaled to unit variance and zero mean, and differences (residuals) between TRW and temperatures were computed for unfiltered, high and low-frequency series (Büntgen et al. 2008). Buffers representing 5^{th} and 95^{th} percentiles of normal distributions were derived to highlight extreme values.

Residuals represent the variability in TRW unexplained by Jun-Jul temperatures when using the scaling approach (Esper et al. 2005). We attempted to explain the residual variability by environmental factors other than temperature (i.e. the modelled sulfur and nitrogen loads). Correlations of TRW residuals (unfiltered, high- and low-frequency time series) with sulfur and nitrogen deposition were therefore also computed.

Estimated historical sulfur and nitrogen regional depositions were calculated according to the method of Oulehle et al. (2016). This method is based on the tightly coherent relationship between measured precipitation, SO_4, NO_3 and NH_4 concentrations from 32 monitoring sites, and Czech and Slovak national emission rates of SO_2, NO_x and NH_3 for the period 1994-2012. Its performance regarding estimated historical emissions suggests this method is robust in the long-term reconstruction and prediction of S and N deposition. We calculated S and N deposition for the period 1950-2010 for each region (KRK, JES, BAB, NT).

Besides pollution, the potential instability in the relationship between Jun-Jul temperature and TRW might also be caused by a changing seasonal window of growth sensitivity to temperature. That is why the 21-yr moving correlations with monthly temperature variables were computed for the months with a presumed influence on tree growth (April to August of the ring formation year, Ponocná et al. 2016). Furthermore, the growing season length was computed for each timberline area according to Paulsen and Körner (2014) – growing season was defined as the period with daily mean temperature higher than 0.9°C and no snow pack. Temperature and precipitation from mountain stations was used and scaled to timberline elevation using the local environmental temperature gradients. For computational details see Kašpar and Treml (2016).

3. Results

Mean values of TRW, mean sensitivity and TRW autocorrelation decrease from west to east (S2, Suppl.). TRW series coherency as indicated by Rbar (Fig. 2) showed widespread depression in the 1950s (all regions) and 1940s (all regions except NT). Peak coherency was achieved in the 1970s (all regions) and the most recent decades (1990 onwards, KRK, JES). Before 1960, mean Rbar was similar among regions, with values between 0.3 and 0.4. Between 1960 and 1970, Rbar increased to 0.6 with the exception of NT, where Rbar continued to be relatively stable.

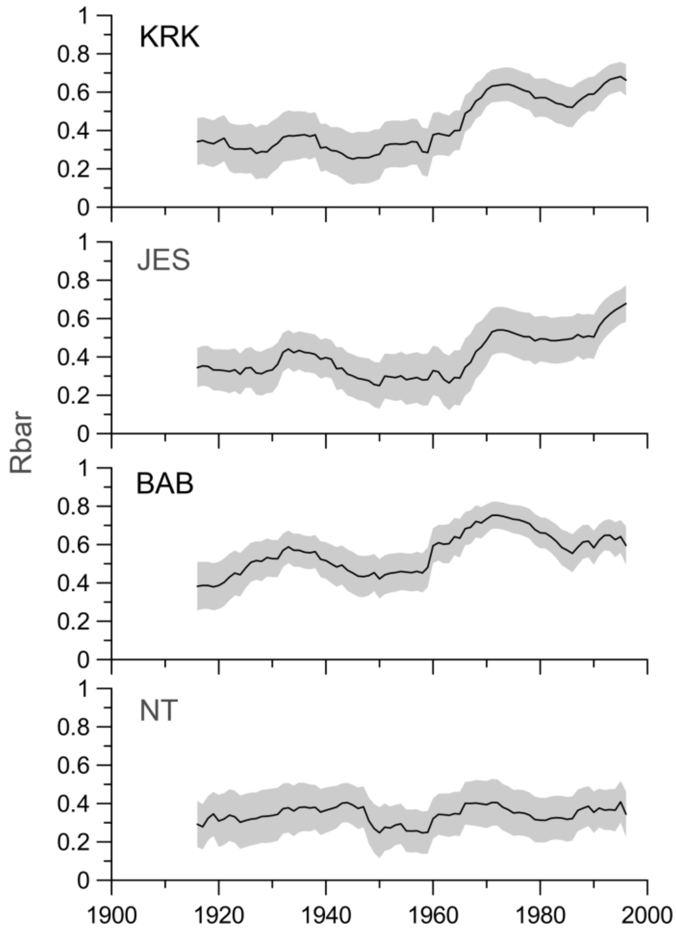

Fig. 2 Coherency of TRW series as indicated by moving inter-series correlations (Rbar). Correlations were computed for 21-yr windows with a 1-yr step. Lines and buffers denote means and standard deviations, respectively.

All SF and BAI chronologies are characterized by two pronounced growth peaks (Fig. 3). The first occurs in the 1940s-1960s, the second in the 2000s. Whereas in the BAB, NT and KRK SF chronologies the first peak is rounded and culminates at the turn of the 1950s and 1960s, the JES and KRK BAI chronologies culminate in the late 1940s and then decrease. The prominent growth depression in the 1970s and 1980s was common to all chronologies, with its lowest point in the early 1980s. The two culmination points of the SF TRW chronologies achieved in the 1940s and 2000s have approximately the same values. BAI chronologies displayed maximum growth in the 2000s (JES, BAB, NT) with the exception of the KRK BAI chronology, which exhibited a maximum growth point in the 1940s. Compared to TRW series, the depressions in Jun-Jul temperature in the 1970s and early 1980s, as well as in the 1920s are relatively minor. The same is true for the positive anomaly in the 1950s. Jun-Jul temperatures attained their maximum values in the 2000s in all regions.

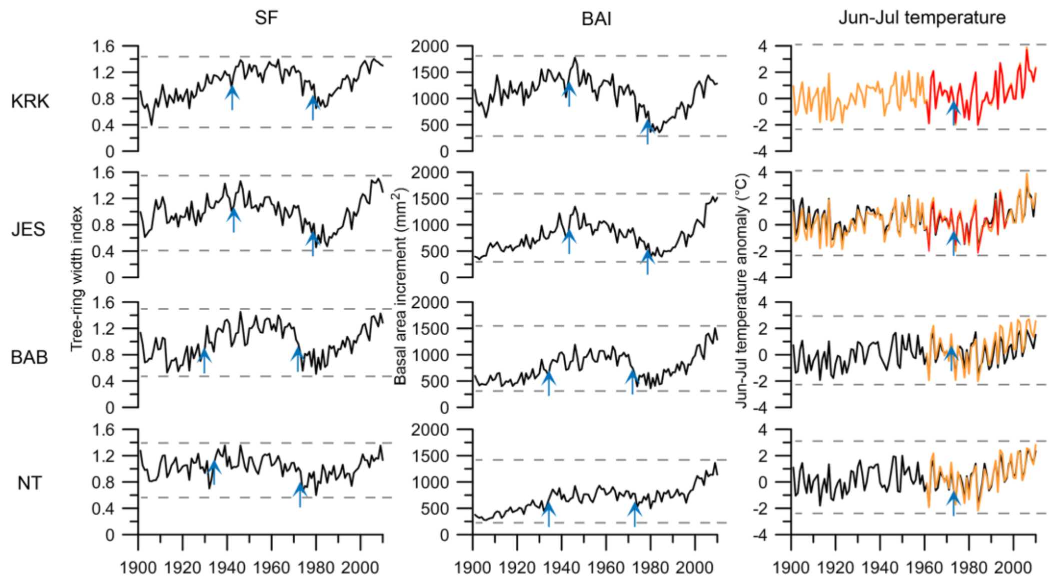

Fig. 3 SF and BAI tree-ring chronologies and Jun-Jul temperatures in the four study regions (KRK, JES, BAB, NT). CRU temperatures are in black, station temperatures are in orange (station data used in analysis) or in red (reference station time series from Sniezka /KRK/ by Migała et al. 2016 and from Praděd /JES/). Blue arrows denote trend breakpoints; dashed lines indicate minimum and maximum values.

Trend breakpoints of tree-ring chronologies are dated to 1943 (KRK, JES), 1930 (BAB) and 1934 (NT) meaning that increasing growth was replaced by a decreasing growth trend (Fig. 3). In 1979 (KRK, JES) and 1973 (BH, NT), the negative trend in TRW indices turned positive again. The only trend breakpoint in Jun-Jul temperature occurred in 1972 or 1973 in all regions.

For unfiltered time series, SF chronologies were, on the whole, slightly less correlated with Jun-Jul temperature (Fig. 4A) than BAI chronologies, with the exception of KRK. In the case of the high-frequency time series, the correlations with temperature were approximately the same as in the unfiltered time series, with only NT showing lower correlation. For time series showing low-frequency variability, there was good agreement between both SF and BAI chronologies and temperature for JES. KRK had substantially better coherence between SF and temperature than between BAI and temperature, the opposite is true for BAB and NT.

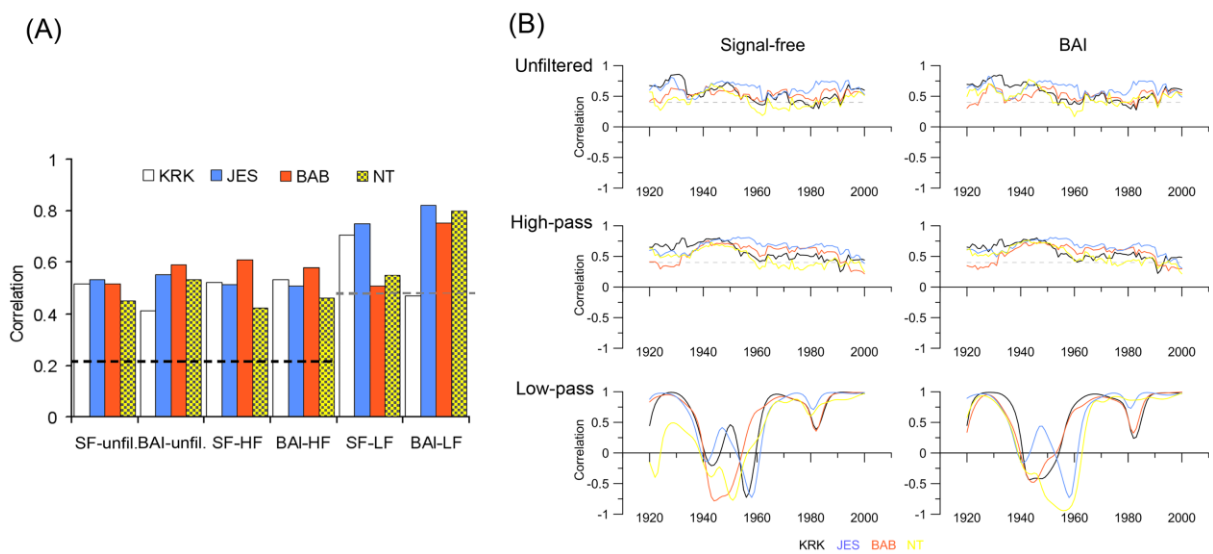

Fig. 4 (A) Correlations of signal-free (SF) and basal area increment (BAI) chronologies with Jun-Jul temperature (1920-2010). Correlations for unfiltered (unfil.), high-frequency (HF) and low-frequency (LF) time series are shown. Dashed lines indicate p = 0.05 with correction for low degrees of freedom of autocorrelated low-pass filtered time series (in gray). (B) Moving correlations between TRW chronologies and Jun-Jul temperature for unfiltered (original), high-pass and low-pass filtered chronologies. The dashed line denotes p = 0.05 (not shown for highly autocorrelated low-frequency time series).

The 21-yr moving correlations of TRW and Jun-Jul temperature between 1920 and 2010 (Fig. 4B) are statistically significant over the entire study period with the exception of NT around 1960 (i.e. 1950-1970 window). Highest correlations were achieved around 1930 (1920-1940 window) and around 1950 (1940-1960 window). Relatively low correlations were found for the period between approximately 1955 and 1980. For high-frequency time series, the correlation decreased slightly from the 1950s onwards with a steeper drop in the 1990s and 2000s. The moving correlations of the low-frequency chronologies showed a pronounced decrease in the 1940s and 1950s for all regions, and a second depression in the early 1980s with a substantial drop for KRK and JES. A less pronounced correlation decrease was observed for BAB and relatively small or almost no (BAI chronology) oscillation for NT.

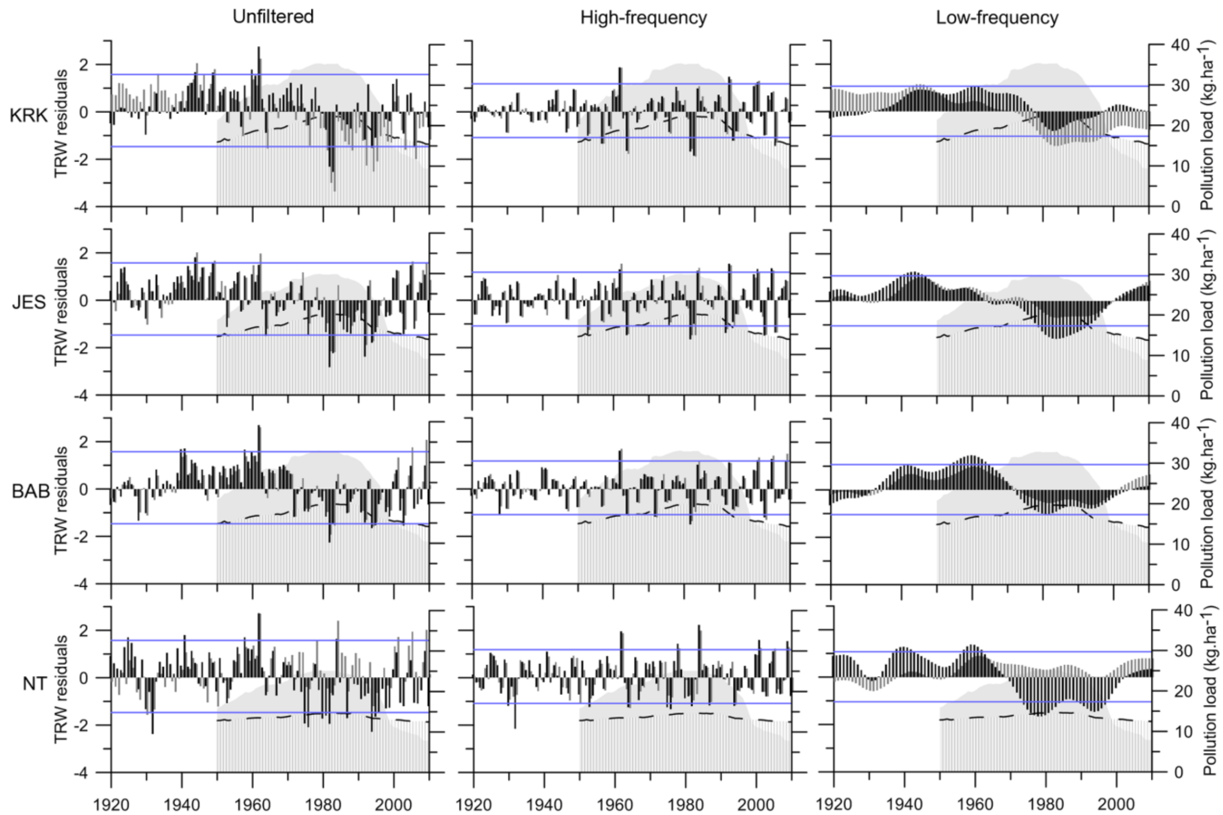

Fig. 5 Departures of tree-ring indices from Jun-Jul temperature for unfiltered, high-frequency and low-frequency time series together with sulfur deposition (gray area) and nitrogen deposition (dashed line and patterned area). Departures of SF chronologies are in black, departures of BAI chronologies in dark gray. Blue line indicates lower (5%) and upper (95%) bounds of confidence limit.

TRW residuals (i.e. chronology departures from Jun-Jul temperature series, Fig. 5) showed a cluster of positive values in the 1940s and 1950s, and negative values between the 1970s and 1990s (KRK, JES, BAB). This pattern is less obvious in NT, where a cluster of positive anomalies in the 1940s and 1950s was interrupted around 1950, and the BAI chronology did not display prevailing negative departures in the 1970s or 1980s. For high-frequency time series, positive and negative departures of TRW from Jun-Jul temperatures are regularly distributed with no obvious clusters. In KRK, however, the two greatest negative anomalies are dated to 1982 and 1983. Low-pass filtered time series are characterized by a greater positive TRW anomaly than Jun-Jul temperature in the 1940s to 1960s (KRK, BAB, NT; 1940s to 1950s in JES), greater negative anomaly in TRW than in Jun-Jul temperature in the 1970s to 1990s, and more recently positive TRW than Jun-Jul temperature (in the 2000s). Low-frequency trends vary between SF and BAI chronologies in KRK and NT. In KRK, negative departures of TRW from temperature are rather limited for the SF chronology in the 1970s and 1980s. In contrast, the BAI chronology shows continuous negative departures of TRW from Jun-Jul temperatures from the 1970s to the present. In NT, the BAI chronology revealed a continuous slightly positive departure from temperature since the 1950s.

Correlations between unfiltered TRW residuals and sulfur and nitrogen deposition were highest and significant for JES and BAB (Fig. 6). KRK BAI residuals were also significantly correlated with nitrogen deposition. The remaining relationships were not statistically significant. In the low-frequency domain (Fig. 6), TRW residuals were significantly correlated with both nitrogen and sulfur deposition for JES chronologies. Nitrogen deposition was also significantly correlated with TRW residuals of NT-SF and BAB-BAI chronologies.

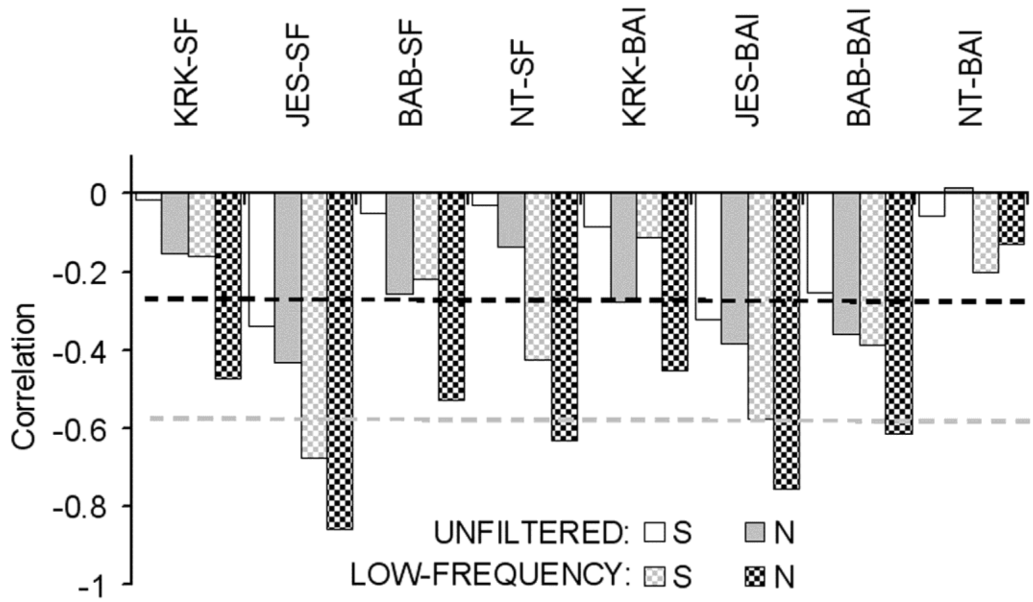

Fig. 6 Correlations of residuals (TRW – JJ; unfiltered, low-pass filtered time series) with modelled depositions of sulfur and nitrogen (1950-2010). Dashed lines indicate p = 0.05 with correction for low degrees of freedom of autocorrelated low-pass filtered time series (in gray).

To further explain clustering of TRW departures from Jun-Jul temperature in certain periods (i.e., trend divergence between Jun-Jul temperature and TRW), the seasonal window of tree growth and the moving correlations of high-pass filtered TRW and temperature variables were computed (Fig. 7). The highest positive TRW residuals in the 1960s coincided with a very long growing season, abrupt decrease in correlations between TRW and June temperature and a short-term high correlation of TRW and August temperature. Short-term increases in correlations of TRW with May (NT, JES) or April (BAB, KRK) temperatures were also observed. In contrast, the highest negative TRW residuals in the 1970s and 1980s were coincident with a very short growing season and a decrease in correlations between TRW and July temperature. In all regions, the periods with a short growing season are characterized by high correlations of TRW with June temperature, whereas the periods with a long growing season displayed high correlations of TRW with July temperature and lower correlations with June.

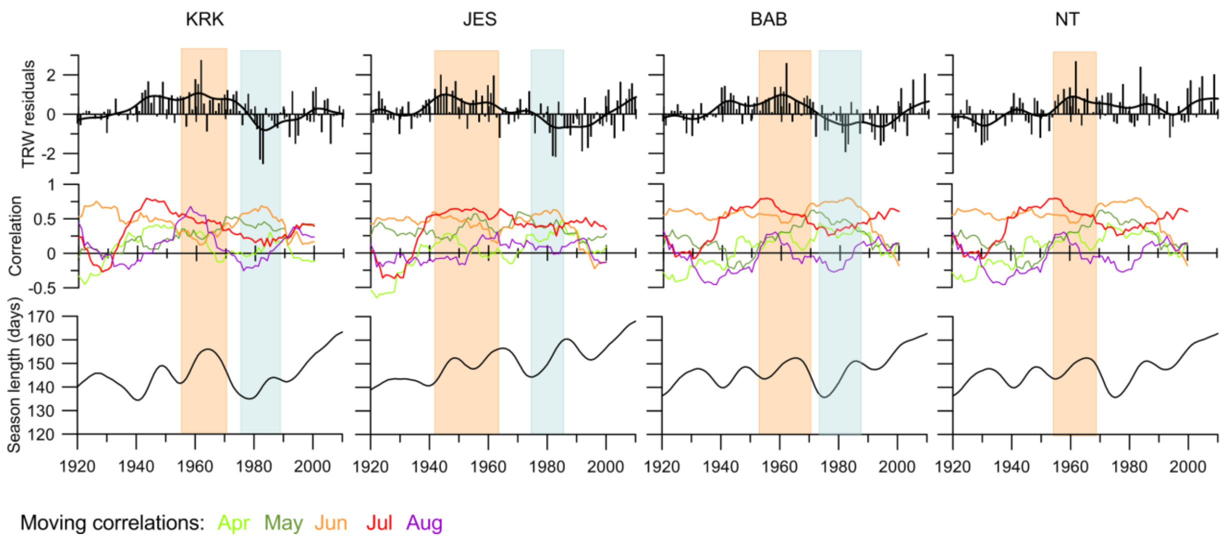

Fig. 7 TRW residuals (unfiltered – bars, low-pass filtered – line) together with moving correlations between TRW and monthly temperature variables and growing season length in each area (Krkonoše, Jeseniky, Babia Góra, Nízké Tatry). Red and blue stripes denote clustered positive (red) and negative (blue) residuals.

5. Discussion

Our treeline tree ring chronologies capturing the period since 1900 showed varying tree growth coherency and variable strength of the relationship between tree growth and summer temperature. Increases in growth coherency were observed in the 1930s (all regions except NT) and 1970s (all regions). The late 1930s contained periods with very short growing seasons. In addition, during the second half of the 1930s, all chronologies revealed rapidly increasing correlations of TRW with Jun-Jul temperature indicating that coherent growth was driven by a common temperature factor. Intra-regional coherent growth patterns since the 1970s were probably a consequence of strong environmental drivers in the form of increasing acid pollution and cooling. Surprisingly, in the period of recent warming after a decrease in acid deposition (1990s to the present), growth coherency continued to remain high (NT), increased further (KRK, JES), or slightly decreased but still remained high (BAB). The recent growth increase common for all trees in KRK and JES is not necessarily driven just by warming, but it might also be supported by newly released nutrients in soils due to enhanced decomposition of organic matter (Kolář et al. 2015). This process has been observed in locations previously affected by acidification, which is not necessarily true for areas with naturally less acidic soils such as BAB or NT.

In all areas, the growth coherency was lowest in the 1950s when shifts in growth-climate responses also occurred. The 1950s represent the second-warmest period captured in our chronologies, with correspondingly high growth rates. Thus, individualistic reactions of growth trends to warming could have been responsible for the decrease in growth coherency. In addition, the period from the 1940s to the 1950s was characterized by complete (KRK, JES) or partial (BAB, NT) cessation of cattle grazing and hay-harvesting, leading to forest encroachment (Kozak 2003, Treml et al. 2016). The localized (i.e. at the site or even the individual tree level) increase in competition or decrease from grazing pressure might then have underlain increasing variability in growth trends during the 1950s.

The analysis of departures of TRW from Jun-Jul temperature revealed their different patterns in high and low-frequency domains. In high-frequency variability, no clustering of residuals was observed, meaning that short-term fluctuations in temperature were reflected in TRW with more or less temporally stable noise and almost no detectable effect of pollution. In contrast, low-frequency time series exhibited systematically higher positive or negative departures in periods with higher or lower growing season temperatures, respectively. From the 1940s to the 1960s, high departures of TRW from Jun-Jul temperature were synchronous with shifts in growth-climate correlations during the period of long growing seasons. An abrupt decrease of the correlation with June temperature and increase of the influence of August temperature were the most apparent. We also observed temporary increases in TRW correlations with April or May temperatures.

We propose that the extension of the time-window of TRW sensitivity to temperature was probably responsible for the detected decrease in climate signal strength. Evidence from on-site measurements of growing season duration at the timberline in KRK (sampling period 2010-2012) supports this suggestion (Treml et al. 2015b). The initiation of radial growth occurred between the beginning of May and late May with the main phase of cell production occurring between May and July, but lasting until early August in the growing season with the highest cell production (Treml et al. 2015b). High cell production rates in growing seasons with an early beginning usually lead to a delay of the end of the cell enlargement phase (Rossi et al. 2013). The window with the greatest sensitivity of radial growth to climate (i.e. the period of cell division and cell enlargement, Kulmala et al. 2017) thus moved considerably. The same could be anticipated for the period between the late 1940s and 1960s. Clustering of growing seasons with prevailing early or late onset of radial growth therefore probably results in shifts in growth-climate response. This is also readily visible in the prevailingly strong responses of TRW to July temperature in long growing seasons and the predominant importance of June temperatures during short growing seasons (with cell division and enlargement constrained to a shorter period).

For unfiltered and low-pass filtered series, the highest negative departures of TRW from Jun-Jul temperature were dated to the late 1970s and early 1980s. Lower growth than expected was a consequence of acid pollution, probably together with short growing seasons and a corresponding decrease in correlation with July temperature (see above). In the 1990s and 2000s, TRW departures turned positive again, indicating the change in growth-climate response (the growing season was the longest over the studied period 1901-2010), which is well supported in KRK, JES and NT. This positive trend could also represent the influence of additional stimulating factors (e.g. nutrient release - Kolář et al. 2015). However, positive departures in the 1990s and 2000s were still smaller than those in the 1950s. Our results therefore show that the recent growth increase has followed temperature increase with only minor deviations, which is contrary to the study of Kolář et al. (2015) suggesting that recent growth enhancement has been much greater than temperature increase. However, in that study the possible TRW chronology bias due to the end effect (Melvin and Briffa 2008) was not considered.

The impact of acid pollution on the climate signal in treeline trees was clear for the unfiltered and low-pass filtered series. The correlations between TRW residuals and acid deposition were strongest in JES and BAB, and relatively weak in KRK, which is the area with the highest pollution load. This discrepancy might be, to some extent, explained by interference from acid deposition and the instability in growth-climate response driven by changing seasonality in KRK. The difference between the growing season length in the 1960s (peak) and 1970s and 1980s (depression) in KRK was the greatest among all regions under study, indicating the most significant shift in the window of TRW sensitivity to temperature.

Low correlations between TRW residuals and pollution load in KRK might also be attributed to a relatively weak reaction of TRW to decreasing pollution and increasing temperature in the 1990s and 2000s when the BAI chronology continued to have smaller values than expected based on Jun-Jul temperatures. These negative residuals reflect inertia in the response of tree growth to soil acidification, because the recovery of soils substantially lags behind the decrease in acid deposition (Hruška et al. 2002). Surprisingly, we also found a stronger response of TRW residuals to nitrogen than to sulfur deposition. However, both substances acidified the environment simultaneously and their effect was probably additive.

For Central Europe, Ponocná et al. (2016) showed that regional differences among treeline chronologies are substantially smaller than among chronologies representing montane forests, and that only in KRK was the effect of acid pollution clearly expressed across the entire elevation range of spruce distribution. The high similarity of treeline chronologies revealed also in our study suggests a strong, although non-stationary, climatic forcing of treeline tree growth, which is able to partially mask the effect of pollution. Vacek and Lepš (1996) demonstrated that acid pollution affects dense stands more heavily than open ones, which could possibly explain the observed pattern of unambiguous pollution impact on (dense) montane forest (Rydval and Wilson 2012, Kolář et al. 2015, Čada et al. 2016) and the less obvious, complex response of treeline stands.

Our study proposes possible causes of growth divergence from summer temperature of treeline *P. abies* in East-Central Europe. It seems that the acid pollution in the 1970s and 1980s was an important but not the only reason for varying divergence of TRW from summer temperature in the 20th and 21st centuries. We suggest that in further studies employing linear transfer functions between temperature and TRW (a typical approach to climate reconstruction, Fritts 1976), the calibration period should be long enough to capture periods with positive and negative departures of TRW from the driving climatic variable. Otherwise, prevalence of positive or negative residuals in the calibration period might distort the resulting reconstructions. This might also apply to estimation of the effect of acid pollution on growth reduction based on calibration of TRW with temperature in periods not-affected by pollution (e.g., Rydval and Wilson 2012). If the calibration window is too short, it might contain a prevailing period of naturally higher or lower growth than expected and thus distort the growth projection in the modelled period. We have also shown that two commonly employed approaches (individual signal-free detrending and BAI) sometimes differ in estimating amplitude and duration of extreme growth episodes. Therefore, any comparisons of TRW and climatic variables will benefit from providing uncertainty estimates that consider instabilities in growth-climate responses (e.g., Büntgen et al. 2010, Treml et al. 2015a).

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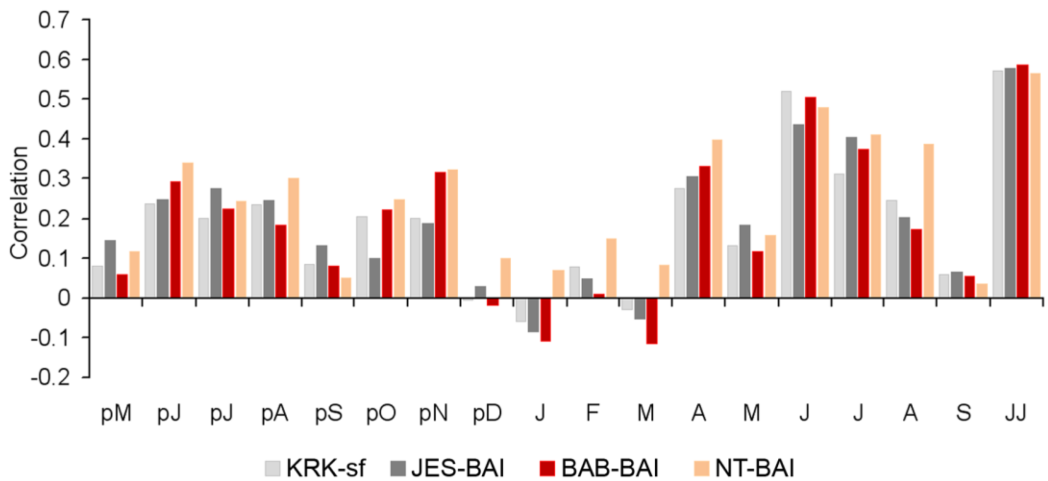
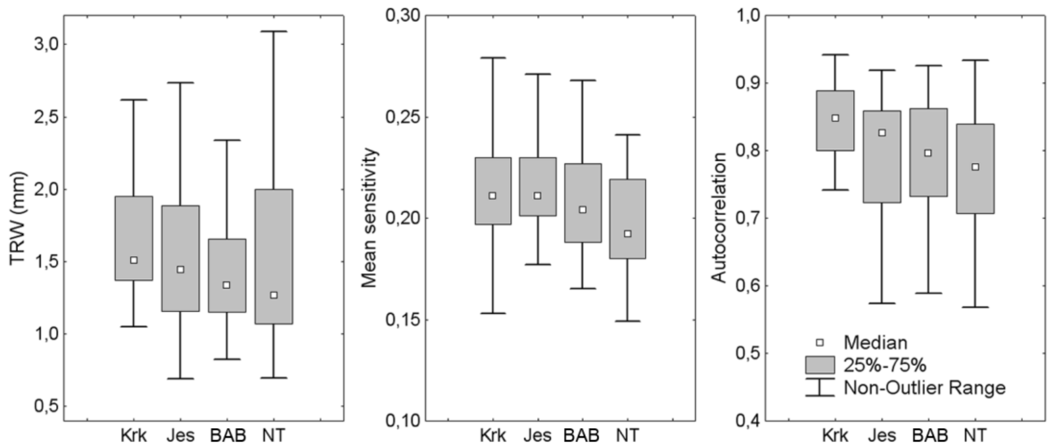
Supplementary files for online publication only

Appendix S1 Correlations between mean monthly temperature and tree-ring width over the 1920-2010 period. Chronologies with highest correlations to Jun-Jul temperature are shown only.



Appendix S2 Basic characteristics of tree-ring chronologies. TRW from KRK is significantly wider than TRW from BAB; the remaining differences are not significant ($p<0.05$, ANOVA, Tukey post-hoc test). Mean sensitivity of TRW series from NT is significantly lower than sensitivity of TRW from KRK and JES. TRW series from KRK are significantly more autocorrelated than series from BAB and NT.



TRW (mm)
3,0
2,5
2,0
1,5
1,0
0,5
Krk
Jes
BAB
NT
Mean sensitivity
0,30
0,25
0,20
0,15
0,10
Krk
Jes
BAB
NT
Autocorrelation
1,0
0,9
0,8
0,7
0,6
0,5
0,4
Median
25%-75%
Non-Outlier Range
Krk
Jes
BAB
NT